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# ECOLOGY

## ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

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## MATHEMATICAL SYSTEMATIZATION OF "ENVIRONMENT," "ORGANISM" AND "HABITAT"

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### I

### MATHEMATIZATION OF ECOLOGICAL THEORY AND THE SYSTEMATIC COLLECTION OF DATA

*"Structural Correspondence" of Experimental Phenomena and of Theory.*— The theoretical formulations of the physical sciences permit of predictions on paper which are accurate for considerable distances. It is to be inferred herefrom that their structure corresponds closely to the structure of physical experimental phenomena. In present-day ecology, however, predictability—the criterion of "exactness" in science—is extremely low. And it is to be inferred that the structure of its theoretical formulations has far less correspondence to the structure (Korzybski, '33, pp. 247–69) of ecological experimental phenomena.[2]

The following is an unanalyzed, "macroscopic" description of the sort of thing that is meant by "structural correspondence": Out of the complex mixture, air, Priestley in 1774 isolated a chemo-physical process which he called "dephlogisti-

[2] This correspondence is not assumed to be like that between molecules and laboratory models of them, nor is it assumed to be like the correspondence between two theories. The correspondence of theories and experimental phenomena is multifarious, and is described under "semeotechnical" processes.

cated air." Lavoisier discovered some mathematically constant features of dephlogisticated air which permitted accurate prediction. Thus Lavoisier created a formulation whose structure we infer to be quite similar to the structure of this chemo-physical process. Stated more specifically, this formulation, which Lavoisier called "acid former" or "oxygen," corresponded (to some extent) to the structure of the somewhat operationally homogeneous chemo-physical process, oxygen. Since the day of Lavoisier various functionally more constant forms of oxygen have been isolated. Corresponding to these forms the notion "oxygen," has been broken down into operationally more constant formulations. These are "oxygen atoms," $n$ "O"; "oxygen molecules," $n$ "$O_2$"; "ozone," $n$ "$O_3$"; and, possibly, $n$ "$O_4$."

In ecology we of course recognize functionally distinct processes such as plants, animals, succession, migration, symbiosis, parasitism, etc.[3] But we have only the loose, descriptive terms, "plants," "animals," "succession," "migration," "symbiosis," "parasitism," etc., which do not accommodate themselves closely enough to concrete processes—of which no two are ever alike—to permit us to construct accurate equations; that is, to construct formulations which can be manipulated to give accurate prediction in concrete situations.

Before we can attempt experimental prediction it is necessary to carry out a

[3] For reasons described hereafter all objects are here regarded as processes having a macroscopic and a sub-microscopic, electronic aspect.

change in the predicting apparatus, ecological theory. For it is no more possible to make present ecological theory produce accurate predictions than to make a wild cherry tree produce fancy dessert cherries.

*The Two Principal Kinds of Change of Theory.*—Semanticists have observed two kinds of change which comprise the evolution of the theory of "exact" sciences.

(1) In the first, no change of linguistic habits, of "logical categories" occurs. An example hereof is the case of dephlogisticated air—"oxygen" described above, whereby descriptive chemistry was transformed into "exact" chemistry. In this case the creation (or the isolation) of an experimental process—dephlogisticated air—came first, and its structure was simulated in theory afterwards. Theory was altered to correspond to the structure of experimental phenomena. A standard example of the converse (the reification of a scientific theory) is Mendeleeff's theoretical formulation of the periodic arrangement of chemical processes which permitted the prediction and subsequent experimental isolation of scondium, germanium, gallium, and Sir William Ramsey's prediction and subsequent isolation of krypton, xenon, and neon. Such changes can be understood and accepted easily by almost everyone who thinks in the conventional manner of the given scientists' society at the time of the change.

(2) The second kind of change does involve a transformation of "logical categories," of language. Such changes are more profound and less easily understood by the given scientists' compatriots at the time they are first invented. An example hereof occurred a few years ago when physicists found that light does not travel with infinite velocity and that there is an apparent shift in the position of stars near the sun's disc. These phenomena were baffling, not because they necessitated the first sort of change of theory, which is an every-day occurrence in physics, but because they could not be dealt with at all

without a change in *language,* in "logical categories," in the organic structure of general thought processes.[4] To accommodate the structure of theory to that of experimental phenomena this time, they had to induce a change in theory by way of language itself. The component of physical language called "three-dimensional geometry" was replaced by "four-dimensional geometry." (And, since Einstein is working on a five-dimensional representation, this may soon occur again.) Once this was accomplished, however, they found it possible to predict all the old phenomena, the new ones on which they had been working, to systematize quite unexplained processes such as the perihelion of Mercury, predict new ones such as the shift of spectroscopic lines in a "gravitational field" toward infra red; and today they are predicting and systematizing important new data with extreme rapidity.

*Mathematical Categories; Language.*—While the data of physics have been growing more complex by leaps, physical theory has become more exact, also by leaps. Non-linguistic increases of "exactness," due to increased precision in measurement and in the amount of system with which data have been collected, have contributed greatly to this increase in precision. But the factor which has changed with a variability and saltation which seems to be most clearly correlated to the variability and saltation of the exactness of physical theory has been the change of language, which has not merely kept constant, but actually increased predictability in physics.

At least one reason why such linguistic changes could occur here and could not occur in ecology is, that the language of physics, unlike that of any of the descrip-

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[4] Such changes hardly occur at all from one Indo-European language to another, for these are dialects whose "logical categories" are identical, *i.e.* "Aristotelian." Only the contrast of Indo-European and, say, Malayalam, Yucatec, Quichua and the like could even faintly approach the change of "logical categories" which had to be encompassed in the theory of physics.

tive sciences, is mathematical. For mathematical language is functionally more constant and more adjustable in structure to the most accurate data "here-now" than any other. Hence, when new data appear, to which the structure of a given form of this language cannot be accommodated, the whole form can be reorganized until its structure corresponds to both the old and the new data. Linguistic reorganization, having itself become a method, "structural correspondence" can now be achieved in the physical sciences without a *break* in method.

Mathematics is here conceived to be and to work in something of the following manner: Our numerical system and our various metric systems constitute an array of raw materials from which can be fashioned any number of formulations. By virtue of the minuteness of decimals— which is potentially infinite—and of the potentially infinite alterations in the size of available metric units, natural numbers and metric units can be formulated to correspond almost as exactly to those aspects of experimental phenomena as our senses and instruments are able to ascertain them. And real numbers, being continuous, can be adjusted to correspond *exactly* to the "here-now" countable and measureable aspects of experimental phenomena. Thus mathematics can be used as an exact descriptive language which is highly concrete. To paraphrase Bridgman quite loosely:—From the point of view of operations the framework of Cartesian geometry . . . is really a physical framework, and what we mean by spatial properties is nothing but the properties of this framework. When we say that space is Euclidean we mean that the physical space of meter *sticks* can be described in Euclidese. It is meaningless to ask whether *empty* space can be described in Euclidese. Geometry, therefore, in so far as its terms are expected to apply to the external physical world, and in as far as it is not a logical system built up from postulates, is an experimental science. (For the original form of this quotation

which is somewhat different, see Bridgman, '32, p. 67.)

Verbal languages, of course, are also based upon an array of materials—words —from which can be fashioned very large numbers of formulations. Verbal, like mathematical formulations, can correspond more or less closely to experimental phenomena; and they can also fail to correspond to them. That is, verbal and, to a much greater extent, mathematical formulations, can be applicable *wherever* the phenomena in question occur (*e.g.* Einstein's geometry); they can be applicable only to *some* processes *at some* velocities (*e.g.* Euclidean geometry); and they can be quite *unapplied* " here-now" (*e.g.* Riemannien geometry at the time it was invented). It makes no difference to the functioning of a mathematical or verbal formulation whether, historically, it was constructed expressly to deal with a body of data. But there is a functional difference, and a sharp one, between mathematical formulations and verbal accounts which are *not known* to correspond to experimental phenomena "here-now," and those which *are known* to correspond to experimental phenomena. As Eddington says ('29, p. 162) "No one questions the advantage of an unfettered development of geometry. But only in so far as this subject is linked to the quantities arising out of observation and measurement, will we find mention of it in a discussion of the Nature of the Physical World."

If we are seriously intending to mathematicize ecological theory we must be clear as to whether we are thereby *transforming* its formulations, or are *mixing* in a new science. Just so, to use an analogy, when we domesticate a cherry tree we must know whether we are changing the plant's somatic structure—say by the use of colchicine—or whether we are merely grafting branches of a domesticated variety onto a somatically wild tree.

This question can be decided quite clearly: If, as is implied above, a science consists of a system of experimental phenomena *to which is linked* a theory with

corresponding structure, then a theory taken *by itself*, whether mathematical or verbal, is still a theory, and cannot be defined as a science (Bridgman, '34)—though it might perhaps be called a *subject* (Eddington, '29). There are cases where mathematics and verbal accounts constitute entirely autonomous theory. However, these occur only where they contain uninterpreted terms. The autonomous theories do not even constitute components of scientific *theory*. In such cases (*e.g.* uninterpreted mathematical system-forms and surrealist fiction) there is little if any direct participation in the performance of *biological work* as it is mathematically defined in this system. Functionally speaking, uninterpreted mathematical system-forms constitute a form of mental gymnastics. At a different place and time they may possibly be found to correspond to the structure of some experimental phenomena and, both by definition and function, become interpreted mathematics. But on the above three counts they themselves cannot be classed "here-now" either as science or as scientific theory until such a time. Interpreted mathematics, on the other hand, constitutes the most general, most functionally constant structural component of scientific theory. It is not added to or introduced into this theory, but is a mode of theoretical representation (Carnap, '34; Quine, '36). Mathematization of a scientific theory is not an addition to it, like a graft on a wild tree, but a change in the nature, figuratively speaking, of the polyploidy induced in some plants by colchicine, in the nature of a somatic transformation. In the case of mathematical ecology, to paraphrase Bridgman ('32, p. 67), the framework of Cartesian geometry would be—not a physi-ecological—but a *bio-ecological* framework, and what we would call spatial properties (or properties of the manifold) would be nothing but the properties of this bio-ecological framework. Hence we can speak just as meaningfully of mathematical ecology as of mathematical physics.

Mathematization is to be regarded as a normal phenomenon in the course of the development of any science. "The less a science is advanced," says Quine ('36, p. 90) "the more its terminology tends to rest on the uncritical assumption of mutual understanding. With increase in rigor this basis is replaced piecemeal by the introduction of definitions. The interrelationships recruited for these definitions gain the status of analytic principles; what was regarded as a theory about the world gains the status of a convention of language." In ecology, primarily for linguistic reasons, observation of experimental phenomena has been going on for an extremely long time with relatively minute corresponding development of theory (see footnote 5). Together with anthropology and the social sciences, ecology has therefore remained a predominantly descriptive science, long after the physical sciences have—by dint of many great, leap-like linguistic transformations—been converted into nomothetic, law-formulating sciences. For ecology to become such a science at this stage in scientific growth, a very extensive, drastic linguistic transformation is unavoidable. For ecology to become an "exact" science in this day of relativity physics, all its basic notions will have to be redefined and stated in such ways as to be fairly functionally constant, and amenable to progressive regulatization. Concretely, they will have to be organized as a system of mathematically expressed descriptions and inferences, as a calculus whose propositions are the constants abstracted from systematically collected ecological data.

*The "Cartesian Co-ordinates" of Ecological Theory.*—Quite obviously, a reorganization of theory by itself cannot convert ecology into a relatively exact science. Such conversion occurs only to the extent to which data are systematically collected—as they have been in the "exact" sciences—giving us an empyrical "Cartesian framework"; specifically, giving us accurate sequences of quantity that will be efficient in theoretically represent-

ing presumably functionally constant types of phenomena. Only to that extent will we have a fairly exact science, for only to that extent—by substituting systematically observed constants and variables into the general theoretical equations for given types of phenomena—can we predict the dynamic balance of forces in any concrete experimental situation. And this is the criterion of a theory's exactness.

However, the moment ecological theory begins to be systematized, the extension of ecology, and thus of the phenomena to be observed systematically, assumes universal proportions. Taylor ('37) describes ecology as follows: "Ecology is not connfined to animals, neither is it limited to plants. Indeed, ecology is not a restricted subject. In its very essence it is comprehensive. Its stimulating key words are, integration, *Einheit,* correlation, coordination, synthesis." This idea of the scope of ecology is corroborated by Allee's and Park's definition of "environment" which is adopted below as useful: "The environment of any organism consists of everything in the universe external to the cells and intimately utilized cell products of that particular organism." Since we must include in the subject matter of ecology the "cells and intimately utilized cell products" themselves (the "organism") ecology is inevitably as broad in scope as Taylor has intimated. Significantly, a similar notion is formulated by a physicist who even hints at the sort of mathematics in which his universal science may be expressed: "An ideal shines in front of us," says Eddington ('29, p. 136), "far ahead perhaps, but irresistible, that the whole of our knowledge of the physical world may be unified into a single science which will perhaps be expressed in terms of geometrical or quasi-geometrical conceptions." This "physical world" (Eddington) is, of course, *contained* in the "comprehensive" (Taylor), in "environment-organism" (Allee and Park). And, to the best of my knowledge, the only kind of geometry that could express all of this

together is a version of $n$-dimensioned geometry (Riemann, '23). Namely, that version in which $n$ is equal to a number of dimensions which seems adaptable to our data ("here-now") of living and non-living components of the "universe."

However, this formulation must wait. Systematization of the vast potential ecological theory here revealed, with the rigor implied by the word "geometry," does not seem feasible yet, and I shall not try to do it here. What I shall try to do in this article is to examine the current definitions of some basic ecological formulations, show their functional variance—if they prove to have such—and restate them in a more rigorous form, with orderable "logical categories." The formulation of the problem may possibly render it amenable to the normal process of evolution described above by Quine. And the constructs not only of ecology, but of all the descriptive sciences may conceivably become rigorous if the recasting of unorderable logical categories into orderable forms is adopted as a conscious method of procedure. Under this treatment the present collection of what Hutchins ('34) calls "Blizzards of data" might become unsatisfactory to non-physical scientists, and might therefore automatically be transformed into a collection of what Hildebrand ('39) calls "The kind of data which would provide honest and crucial tests for any theories." That is, the present unorderable collection might possibly be recast into an orderable one. And it is to be hoped that it will, for only when this occurs may we reasonably hope to become as efficient in social and psycho-biological matters as we already are in chemo-physical affairs.

## II

### ANALYSIS OF CURRENT DEFINITIONS OF "ENVIRONMENT," "ORGANISM," AND "HABITAT"

*"Environment."*—The most recent authoritative definition of "environment" which I have been able to discover was

formulated by Allee and Park ('39). It reads as follows: "The environment of any organism consists of everything in the universe external to the cells and intimately utilized cell products of that particular organism." This definition is here adopted as useful. The modification which follows it, however, cannot be accepted because it is in contradiction with the well substantiated theory of relativity. It reads as follows: "No part of this environment is without potential effect on any organism, although some phases have such a direct importance that they are regarded as comprising the effective environment." This notion cannot be accepted because of the vast and demonstrated regions in the universe which are without any potential effect whatsoever upon any given organism or group of organisms. The formulation of one of these regions, which was theoretically demonstrated by Einstein, is accepted by Bridgman ('32, p. 67) and most other physicists, and is illustrated in the following figure (fig. 1) based on Eddington
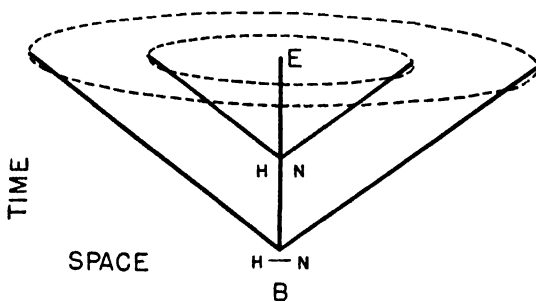


FIG. 1. Diagram of space-time region around any organism beyond whose limits no process can effect the organism.

('29, p. 48). In this figure, let $B$ indicate the location in space-time of any given organism's beginning such as, for instance, the union of sperm and ovum; and let $E$ indicate its end as an organism, its "death." The perpendicular line joining these two points will then indicate the space-time extensions of the organism. (No significant widening or other form of curvature of this line in space-time can be shown here because the scale is so small

that even the farthest-roaming organism's spatial extensions are too minute to show up here.) The cones represent two of an infinite number of states of a steadily shrinking region. This is the region within which the fastest-moving process— light, travelling at about 300,000 km. a second—can start, at any point-instant ("Here-Now") during the organism's existence, and effect it before its end, $E$. The two stages of the region shown on the diagram happen to be its largest extension and a very much smaller one which is shown to exist at the spatio-temporal midpoint of the organism's life. But any others could be shown.

Given systematically collected data, similar cones could theoretically be constructed for all the processes in the entire environment ("universe"), and it can be demonstrated as a rough elementary formulation that all processes at a greater distance from any organism than the combined average convergent velocity of process and organism times the organism's remaining length of life are absolutely discrete from the organism and have no potential effect upon it whatsoever. This region is equal to a geometric hyperbody, defined below as "habitat," and, of course, constitutes part of "environment."

Besides this discreteness in space-time there is absolute discreteness between "organism" and parts of "environment" due to structure. This situation will be decribed in connection with the systematization of "society." Moreover, there is absolute discreteness due to the great quantities of even near-lying structurally continuous processes. These processes may be so abundant that a given organism cannot be a function of more than a minute fraction of them (e.g. a queen bee in relation to all but one drone). Being analogous to the phenomena dealt with in field theory this discreteness can be measured only statistically.

"Organism."—It is impossible for me to quote a current definition of the central ecological formulation, "organism," for I have found none in any modern

ecological publication, text, or glossary whatsoever, nor as a matter of fact is the term so much as listed even in the Encyclopædia Britannica. And what is more important, competent ecologists whose attention I have called to this situation believe that there is no functional definition in current use, and that today this term still "Rests on the uncritical assumption of mutual understanding" (Quine, '36). I shall therefore not expend space upon its discussion.[5]

"*Habitat.*"—I have gone through a large number of current definitions of "habitat" including those contained in Carpenter's ('38) "Ecological Glossary," and have chosen two which seemed to be typical of all, and to be good illustrative material as well. The first definition, by McDougall ('27, p. 229), reads as follows: "By the habitat of a plant or plant association is meant the kind of situation in which the organism lives. It is practically equivalent to what would be meant by the immediate environment. It is the place of abode of the organism together with all the environmental factors that are operative within the abode. The term may be applied to any area which is characterized by uniformity of at least some environmental conditions, such as a ravine, a bog, or a south-facing slope."

The second definition (Weaver and Clements, '29, p. 163) reads: "Every part of the environment that exerts directly or otherwise a specific influence upon the life of the plant is a factor of the habitat." Also, "The habitat, *i.e.*, the kind of place in which the plant grows."

The commonest element of definitions of "habitat" is: "The kind of situation in which the organism lives"; "The kind of place in which the plant grows"; "The place of abode of the organism"; and also by implication, "Uniformity of at least some environmental conditions." First of all, such formulations almost invariably represent not the whole possible process range of which the "organism" is a function, but to a greater or lesser degree, a partial, and in part an accidental range which happens to be acting upon most individuals at the moment of definition, a range which could be greatly extended: *e.g.* the introduction of rabbits in Australia. Furthermore, laboratory experiments have frequently shown that processes whose uniformity was formerly regarded as essential to the operations of an organism could be altered quantitatively (slowed down or speeded up) and qualitatively (in respect to order and direction) far beyond the accidental range of all existing "spontaneous habitat" processes whatsoever: *e.g.* fertilization of mouse ova *in vitro* (Pincus, '36); the use of oxygen-helium mixtures instead of air for deep sea diving; the common nutrition of plants in nutrient solution instead of soil, their watering by sprinklers instead of rain, and their irradiation by electric lights instead of the sun (C. Ellis and M. A. Swaney, '38). And finally, the "Kind of place, abode, or situation in which a plant lives" almost always includes an undetermined quantity of processes which are structurally and statistically discrete from the organisms in question; *e.g.* all but a few electromagnetic wave lengths or a few cubic meters of soil in relation to plants.

We may summarize the situation by saying that in actual practice current defi-

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[5] The dictionary definition is descriptive and circular: "*Biol.* An individual constituted to carry on the activities of life by means of parts or organs more or less separate in function but mutually dependent; any living being." Or it is intensional: "*Philos.* Any thing or structure composed of distinct parts and so constituted that the functioning of the parts and their relations to one another is governed by their relation to the whole" (Webster's, '39). There seems to have been no significant advance to date over definitions in use about a century ago. One used in 1842 reads as follows: "Organism: An organized body, consisting of mutually connected and dependent parts constituted to share a common life; the material structure of an individual animal or plant" (Oxford, '32). This kind of definition thus appears to be analogous in the realm of semantics to what is called, in the realm of biology, a "Persistently primitive type" (Lull, '29, pp. 185–6).

nitions of "habitat" simply describe what happens to exist in an organism's space-time or geographical vicinity, thus excluding some processes of which it can, and including some processes of which it cannot be a function. Consequently such definitions cannot possibly become part of the functionally constant general formulations (equations) of which both spontaneous and artificially adapted "habitats" must be only special cases. Besides being themselves unorderable (geographic instead of functional), such definitions of "habitat" are obviously based on the unsystematic and therefore largely unorderable sort of preliminary data which have not and cannot lend themselves either to the formulation or the testing of systematic ecological theory.

This concludes our analysis of three formulations which constitute a large part of the framework of current ecological theory. It would not be very difficult to demonstrate that important correlations cannot be established between these terms. The functional inconstancy of "environment" and "habitat" and the absence of any formulation whatever of "organism" has structural implications which would ramify throughout and vitiate any systematic ecological theory if they could have constituted parts of one. In fact these implications would be found to be so fragmentary and so vastly contradictory that—in view of the great need—the *nonexistence* of such a theory is no doubt largely a function of what evolutionists call their "unprogressiveness" (Lull, '29, p. 193); that is, in the case of scientific theories, the unorderability of their logical categories.

### III

#### MATHEMATICAL ECOLOGICAL THEORY

*"Environment."*—"Environment," the "comprehensive," has been defined above as, "Everything in the universe external to the cells and intimately utilized cell products of the particular organism in question." The conventional mathemati-

cal term for this sort of notion is "manifold."

For lack of better names the operationally constant processes constituting "environment" will here be called "entropic," "bio-catalytic," "signalloid," and "semeo-technical." And the relationships between them are conceived to be mathematically describable: Entropic processes are regarded as, by and large, the most basic and the simplest of all. Their changes of each other can in general be described by differential equations of the lowest orders. In "environment," however, not all regions are entropically structured. (And this will be proved below to the satisfaction, I hope, of any chemist or physicist.) There are, for instance, regions known as "plants," composed of integrated entropic and of bio-catalytic processes (Henderson, '13, pp. 130–31), which are here regarded as changes of certain changing entropic processes; as changes of changes. Thus they are seen to be, in general, describable by differential equations of higher orders. "Animals" are defined as integrated regions composed of certain entropic, bio-catalytic, and signalloid processes. Since signalloid processes are regarded as changes of certain bio-catalytic processes they are seen, as a general thing, to be describable by differential equations of still higher orders. And "men" are defined as integrated regions composed of semeo-technical as well as of the first three orders of process. Here semeo-technical processes, being viewed as changes of certain signalloid processes, are seen to be theoretically describable by differential equations of the highest observed orders. These four categories are, of course, highly interlocked. A given bio-catalytic derivative, for instance, while describable by equations of higher orders than certain entropic derivatives, still may be of lower orders than other entropic derivatives; and similarly with the others.

The variously structured regions of "environment" known as "non-living systems," "plants," "animals," and "men"

are, theoretically, seen to be describable at any given time by *integral* equations of corresponding orders. For, to use a mathematical term, they constitute singularities within "environment" just as do entropic systems in Einstein's space-time manifold (Eddington, '29, pp. 127–29). In the theory of relativity the moving sun and planets, for instance, are regarded as singularities within space-time. They are mathematically described as unusual but definite curvatures, as puckers in space-time. Taken together, these unusual curvatures constitute the general condition, the structure of their region in space-time. If the behaviors of the formulations "sun" and "planets," which are functions of this general structure of the space-time manifold, are to have scientific value, their structure must correspond to the empirically substantiated structure and behavior of the sun and planets as determined by descriptive, special-process physics. And as a matter of fact, the functions of the singularities of relativity theory not only satisfy these descriptions and special-process laws but, as already stated, explain several phenomena for which no laws could be found by special-process physics. Still broader is the case of general ecological theory which (as defined above) includes the theory of relativity. In the general manifold, "environment," not only "planets," but also "organisms" are regarded as mathematically describable singularities, though we do not yet have all the mathematics necessary for this. Taken together the description of any group of these living singularities is equal to a description of the structure of a region of "environment." Our notions of their mutual deflections and transformations such as "photosynthesising," "eating," "reproducing," and so on, are in all cases regarded as functions of this general structure. In order to have validity, bio-ecological formulations, just as these of what we might call physi-ecology, must also arrange themselves in structure and behavior so as to correspond to the structures and behavior described by the

biological special-process sciences and, if possible, to explain the many phenomena whose laws their theories are not equipped to formulate or to synthesize.

*Multiordinality of the Processes Constituting "Environment."*—An instance of entropic "process" is the eruptions in the region called the "sun." Of bio-catalytic processes there are no instances on the "sun." However, in "plants," "animals" and "men" there are many. Participating herein are processes known as "auxins," "hormones," "vitamins," "trephones," "enzymes," and the like. These processes are not at all entropic in these regions, as some special-process physical scientists might assert, nor are their results entropy. On the contrary, these processes intervene in certain entropic processes and transform them to invariance relative to themselves; that is, transform them into processes which are bio-catalytic. Asher ('37, p. 2) says this very thing in substance, as follows: "Even though the boundaries, within which autonomous [entropic] functioning and [bio-catalytic] regulation may be strictly separated are of varying breadth, fundamentally function and regulation [lower and higher derivatives] are to be kept conceptually separate." It is of the essence of the theory of relativity, of Riemannian geometry, and all the rest of ecologoid theory that processes cannot be analyzed independently of their loci within the manifold. True it is that "hormones," "vitamins" and the like, if boiled in the laboratory, will behave entropically. However, that is true because they do so behave in that locus of the manifold. In their normal loci in "plants," "animals," and "men" they behave as more complex integrals; that is, as bio-catalytic processes, whose function is the enaction of transformation laws, the enaction of the laws of transformation of entropic and other processes to invariance relative to themselves. It is therefore not simply meaningless, but completely false to say that a process is entropic or bio-catalytic or signalloid or semeo-technical irrespective of its locus

within the manifold. In a word, process and locus are invariable functions of each other. Korzybski's insistence ('33, p. 14) upon the *multiordinality* of all formulations is insistence upon this essential of ecological theory. Stock examples of this fundamental relation are afforded by Asher's description of "carbonic acid," "urea," and "gall acids" as behaving bio-catalytically in some loci, entropically in other loci even within living organisms. Such multiordinality is experimentally verified for "boron," "zinc," "iron," and "manganese," which behave bio-catalytically in "plants," entropically in many other loci; and so on (Ellis and Swaney, '38).

*Entropy and Counter-entropy, a Balancing Tendency of "Environment."*— Entropic processes continuously intervene in one another's operations, acting as derivatives of various relatively low orders. The general trend of these interventions is toward lower, more stable organization, the trend known as entropy. "Loss of organization," says Eddington ('29, p. 74) "is equably measured by the chance against its recovery by an accidental co-incidence. . . . The practical measure of the random element which can increase in the universe but can never decrease is called *entropy*. . . . Entropy continually increases. . . . The law that entropy always increases—the second law of thermodynamics—holds, I think, the supreme position among the laws of Nature."

The notion that entropy "continually increases," "always increases," is a generalization based primarily upon the observation of the behavior of gases, and in part of "ideal gases." Boltzmann says in this connection (Klein, '10, p. 91), "As regards entropy, solid and liquid bodies do not differ *qualitatively* from perfect gases; the discussion of the entropy of the former, however, presents greater mathematical difficulties." In spite of these difficulties Planck (after Clausius) did extend this notion, via "ideal gases," to the behavior of solid and liquid en-

tropic processes. And on the basis of these extensions Eddington ('29, pp. 127–29) and not a few other physical scientists claim that the principle of entropy has been extended to *every* body. Planck (1897, p. 97) himself, however, had a different view of his accomplishment. "The time will probably come," he said, "when the principle of the increase of entropy will be set forth by isolated metaphysicians as valid *a priori* outside of its connection with human experimentation. However, there is no effective weapon either for the protagonists or for the opponents of the second law in the struggle for the establishment of its general validity except the ceaseless effort to follow this law's actual contents to its furthest consequences and to bring each of them, correctly formulated, before the judgment seat of the highest judge, experience."

The correctness of Planck's attitude, which Bridgman ('32, p. 7) has formulated as the "operational" attitude of modern physics, was fully borne out, according to Lewis and Randall ('23, pp. 121–22), when, "In the brilliant investigations of Pasteur on asymmetric or optically active substances, it was shown that a system of optically inactive ingredients never develops optically active substances except through the agency of living organisms . . . or as the result of the conscious choice of the experimenter [who is also an organism]. While we admit the theoretical possibility that somewhere, by chance, an inanimate system might develop optical activity, such a case has not been actually observed, and indeed, we know that even when an asymmetric system has once been obtained, it will in course of time become optically inactive through the process known as recemization. On the other hand, countless asymmetric substances are found in animate nature, where indeed a symmetric substance is more the exception than the rule. . . . It seems by no means without the realm of probability that changes which are associated with a total decrease of

entropy may sometimes occur in living things."[6]

To say that a decrease of entropy, a decrease of the random element, may sometimes occur, is a great advance in scientific concreteness over the very widely held theory that entropy *always* and *continually* increases, and can *never* decrease. However, this advance still leaves general ecological theory far from corresponding in structure to the structure of experimental phenomena. In order to secure correspondence it is necessary to proceed much further: According to the formulations of astronomy and geology (Schubert and Dunbar, '33), we regard the earth as having undergone an Azoic period very many millions of years ago, during which it was composed exclusively of entropic processes. No life processes of any sort are conceived to have been included in it, and consequently, the total weight of higher order derivatives is regarded to be equal to zero on the earth for this period. According to the formulations of palaeontology the Azoic was followed by the Archeozoic part of the Pre-Cambrian period during which the total weight of bio-catalytic, and possibly of signalloid derivatives, though low, was above zero. And, not to labor the obvious, present-day observation shows that the total weight of higher derivative processes—and this includes not only bio-catalytic, signalloid, and semeo-technical processes, but also very extensive, complex organic compounds, *e.g.* coal, oil, humus, built up by counter-entropy and not yet completely recemizated or otherwise "disorganized"—are relatively enormous, weighing billions of tons. From these observations, which are corroborated by bio-chemical observations on optically active substances, we are not merely safe in inferring, but are forced by overwhelming scientific evidence to infer, that in the loci of the higher deriva-

tive processes which are included in "plants," "animals," and "men," many entropic derivatives such as "oxygen," "water," "carbonic acid," "nitrogen," "electromagnetic waves," and so forth, are transformed to invariance relative to these higher derivatives, becoming ever *less* random and *less* stable. This is, both functionally and by definition, a counter-entropic trend. And this trend we call "life."

The *mechanism* by which the second law's principal effect of universally increasing mixture and multifariousness gives rise to opposite results, called entropy and life, is as follows: In entropic processes the concomitant of increasing multifariousness is increasing stability. "What usually happens at the impact (of a stone or other "mechanical object") is that the molecules suffer more or less random collisions and rebound in all directions. They no longer conspire to make progress in any one direction; they have lost their organization. Afterwards they continue to collide with one another and keep changing their directions of motion, but they never again find a common purpose. Organization cannot be brought about by continued shuffling. And so, although the energy remains quantitatively sufficient (apart from unavoidable leakage which we suppose made good), it cannot lift the stone back. To restore the stone we must supply extraneous energy which has the required amount of organization" (Eddington, '27, p. 70). Since such energy is available for entropic processes only by exceedingly rare chance, increased stability is a concomitant of entropy. Consequently there appears to be a "Running-down of the universe" (Eddington, '27, pp. 63–86).

However, for bio-catalytic processes the concomitant of increasing multifariousness is increasing *instability:* "The indifference of effect of hydrogen and carbon, upon the properties of the molecule," says Henderson ('13, p. 218), "is undoubtedly a principal cause of the stability of complex organic substances. Through this

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[6] Other observations of this sort have been made by G. N. Lewis, August Kekulé, and, no doubt, other physical scientists.

peculiarity of the two elements the integrity of the valence energy of carbon is preserved, and the long carbon chains are possible. Whenever the molecule becomes overloaded with radicals of other kinds [increased multifariousness] the strength of the tie between carbon atoms diminishes *and the compound becomes unstable.*" And again, "Organic substances are uniquely fitted not only to provide complexity of structure [increased multifariousness] to the organism, but also through their *instability* and manifold *transformations,* to endow it with diverse chemical activities, with complexity of physiological function" (Henderson, '13. Italics mine). *The "shuffling" in living processes constantly increases the organism's multifariousness. Through this very process itself, it automatically receives,* in the words of Eddington ('27, p. 70), *a "supply of . . . energy which has the required amount of organization."* And "organization" means that the molecules "conspire to make progress in any one direction." *Moreover, unavoidable leakages are hereby automatically "made good"* (Eddington, '27, p. 70). All this occurs through the "intervention" (Asher, '37) of bio-catalytic processes in certain entropic processes within regions called "plants" and also in the other organisms with which we shall deal later. "Given an enzyme possessing the power to select and catalyze any one of the reactions," says Henderson ('13, pp. 230–31), "the formation of any special one of the possible products in comparative purity ["conspiring to make progress in one direction"] is an automatic result. Such processes are in nature carried out with a perfection which to the chemist is almost inconceivable, by means of structures of the highest intricacy." Moreover, "the body may carry on such (metabolic) processes in the greatest variety and complexity, rearranging and modifying its chemical structures to any extent, and there never will be an appreciable wastage of precious material or of equally precious energy in the process" (Henderson, '13, p. 237).

And finally, "In the highest degree, the organism possesses the power, by enzymatic catalysis, to select any one of a group of simultaneous reactions . . . and make that one predominant ["progress in one direction"]. . . . The unique . . . adaptability of the [entropic] process and the unique chemical [bio-catalytic] powers of the living organism interlock" (Henderson, '13, pp. 231–32). This interlocking constitutes the relation of one form of a host of more or less nearly living colloidal structures with its "habitat."

Mixtures and combinations of the environment's processes, then, may or may not imply an increase in the random element and loss of organization. In entropic loci they do in general imply greater, less organized stability; in life processes, greater instability; greater and more organized instability. This is the *essential* difference between the increasing multifariousness of entropic process on the one hand, and the increased multifariousness of the higher derivative or life processes on the other hand. This difference between entropy and life, stripped of linguistic confusion, becomes clear and stands out, I think, as the most fundamentally important functional difference in "environment." This formulation may be fallacious. But if it is, then the notion of entropy and the formulation of the second law of thermodynamics must perforce be incorrect also, and that is quite improbable.

Thus far we have discussed bio-catalytically regulated entropic processes, of which only "plants" are exclusively composed. Even the briefest panoramic discussion of signalloid processes will both round out and further substantiate this formulation: The principal function of this higher derivative process is, I think, precisely the same as that of bio-catalysis: "To select one of a group of simultaneous reactions . . . and make one predominate" (Henderson, '27, pp. 231–32). And that one—or those several—are in the main those which "supply . . . energy which has the required amount of

organization," and which "make good un- avoidable leakage" (Eddington, '29, p. 70), thus constituting "life."

It is unnecessary, I think, to expend space here to show that processes rang- ing from typical "ontogenetic," through "instinctive," and up to "conditioned," or "learned" behavior—a range from the highest derivative bio-catalytic to the highest derivative signalloid processes— perform in the main these functions. I shall therefore let the highest of these stand here as the prototype of the rest: "The primary function of the nervous system is obvious," says Pavlov ('28, p. 379). It is, continuously to [help] main- tain a dynamic equilibrium between the functional units within the self-contained system of the organism and between the organism as a whole and its environment. The pre-eminent function of the lower parts of the central nervous system is to integrate the activities of the separate parts within the organism [causing them to "conspire to make progress in any one direction" Eddington, '27, p. 70]. The rôle they play in maintaining the higher animal in equilibrium with its environ- ment [securing the "supply of extraneous energy which has the required amount of organization" and "making good unavoid- able leakages" Eddington, '29, p. 70] is only subsidiary, the most delicate adjust- ments of this equilibrium being pre-emi- ently the function of the (cerebral) hem- ispheres."

The instability of signalloid processes is very great. "Excitation" and "inhibi- tion," "irradiation" and "concentration" (Pavlov, '28, chaps. 22–23) interoscillate with great rapidity in signalloid loci. The question whether there are entropic or bio-catalytic processes which exhibit as variable and rapid changes as do these signalloid, these "electro-colloidal" proc- esses (Korzybski, '33, pp. 115–16), is not certain and is not of crucial impor- tance for this systematization. For, just as it is impossible to say whether a proc- ess is entropic or bio-catalytic without naming its locus in "environment," so

also is it impossible to specify whether a process is signalloid without specifying its locus. For these and many other reasons, which will appear in a subsequent paper, we may regard signalloid processes as higher derivatives of bio-catalytic proc- esses in both their macroscopic manifesta- tions (studied by comparative psycholo- gists) and their sub-microscopic manifes- tations (studied by bio-physicists).

An immediate description of semeo- technical processes would make the hier- archy of derivatives appear more com- plete. Semeo-technation, however, is inextricably connected with "social" phe- nomena and its discussion lies beyond the realm of this paper. As a matter of fact even the discussion of the lower deriva- tive processes will remain exceedingly in- adequate until they are synthesized with "social" phenomena. For obviously the four steps of the process-hierarchy con- stitute one immense, mutually dependent system on the Earth such, that only when they are in "social" conjunction with each other does increasing mixture and multi- fariousness make good unavoidable leak- ages and acquire energy which has the re- quired amount of organization for its self- perpetuation; that is, give rise to the "equilibrium" of which Pavlov speaks above, the equilibrium called "life."

This "equilibrium," the characteristic relation of "habitat" and "organism," is of course extremely dynamic. Its macro- scopic shifts and upsets surge far and wide through the great system, "environ- ment," under many special names such as biological growth and decline, speciation and extinction, evolution, succession, and retrogression. And there is no reason a priori why we should not expect similar processes to have arisen not on the Earth alone, but wherever in "environment" similar conditions may be found.

These considerations of the second law of thermodynamics and its two opposite effects constitute, I believe, another dem- onstration of the scientific axiom that, to use the words of Planck, no principle is "valid a priori outside of its connection

with human experimentation." For now "The law that entropy always increases, [though *not*] the second law of thermodynamics," is lowered from "The supreme position among the laws of Nature" to the only position in which it has been observed to operate: The supreme position among the laws of entropic derivatives.

I think that the ecological view of a universe, not as unopposedly running down, but of a universe in which life is counterposed to entropy is quite logically the first positive contribution of unified ecological theory. And much further development of this formulation can occur through an ever greater synthesis of the theory of relativity-physics, or better perhaps of physi-ecology, with that of bio-ecology within the structure of general ecological theory.

*"Organism" and "Habitat."*—Living "organisms" are defined as integrations of two or more of the principal categories of derivatives, counting from entropic upward. "Organisms" are integrations; and the processes of integration or synthesis constitute their operation, their existence. The synthetic transformation of surrounding processes are not random, but selected and organized in such ways that they conspire to make progress in specific directions. The general average effect of organisms is therefore counter-entropy, is life.

Any given organism's "habitat" is defined as being composed of all processes which affect it, eunomically or dysnomically, in the course of its life. Consequently the boundaries of any "habitat" constitute a group of definite geometric hyperbodies within "environment" on the pattern of the light cone (Fig. 1). (The concrete shapes and sizes of the figures representing the effective regions of the various processes, however, can be determined only after data have been collected systematically.) This hyperbody is identical in principle with the physical construct of field (see Einstein and In-

feld, '38, pp. 129–56), the testbody being the given organism, either in actuality or in imagination. This habitat has a eunomic and dysnomic aspect, relative to the testbody. (Entropic processes, being disintegrating and not self-perpetuating, cannot have a nomic index. For them field is merely positive or negative.) The condition of the organism is a function of both the absolute and the relative densities of these two fields, which will here be called the *ecus* and the *antecus* respectively.[7] For every organism there is a point of antecous density beyond which it disintegrates. This point, in spatial directions, marks the spatial boundaries of the habitat; and in the temporal direction it marks the end of "organism" and, by definition, of the geometric hyperbody, "habitat." The density of both ecus and antecus varies in two ways: (1) as in physics, it is a relation of field mass to area; but (2) unlike physical field, it is also a function of the efficiency of the testbody's (organism's) behavior. *E.g.* the density of the nutritive field of antelopes is equal to amount of grass per square kilometer, plus the efficiency of antelope perception and locomotion. Less efficiently perceptive and locomotive organisms such as domestic cattle perish at the same physical (not ecological) density even when corrected for organism size.

The definition of "organism"—an enduring singularity of habitat which is an integration of two or more of the four basic derivative types, counting from entropic upward—is implicit in that of habitat. This is due to the fact that neither one is absolute. As here defined, many parts of habitats are parts of organisms, many organisms are parts of habitats, and no instance of either is independent of or discrete from at least one instance of the other. And neither definition is affected by the velocity of any changes, as are the current definitions.

[7] "Ecus" is the Anglicized form of the Greek "οικος" (home, country) from which "ecology" and "economics" are derived; "antecus," from "αντοικος" (the house opposite).

The conclusion of this paper brings us near the midpoint of an elementary examination and redefinition of the central categories of ecological theory. Among others, four points raised here remain to be answered in a subsequent paper: (1) That of structural connection and discreteness and, as a special case thereof; (2) that of structural correspondence between theory and experimental phenomena; (3) semeo-technical processes; (4) the systematization of "society."

The claim of this systematization to being mathematical lies in its selection of categories with mathematical, that is, operationally constant relations. Its practical value will, I hope, be demonstrated in the near future through its applications to concrete experiments, for which the systematic collection of data has now been completed.

**.  SUMMARY**

This article is an attempt to make a break in the vicious circle of the non-orderable "logical categories" of ecological theory, an attempt to demonstrate the value of adopting as a conscious method of procedure the recasting of non-orderable, operationally inconstant logical categories into orderable, operationally constant forms.

The first result of this demonstration is the following synthesis of the categories, "entropy," and "life." The second law of thermodynamics implies universally increasing complexity and multifariousness. In some loci of "environment" this leads to an increase in the random element, loss of organization of movement, constantly greater stability and hence, a "running-down" tendency in the universe. Other loci ("plants," "animals," and "men") possess the power to direct their increasing multifariousness by selecting and catalyzing those processes which furnish a supply of energy which has sufficient organization and sufficiently makes good their unavoidable leakages to perpetuate and increase themselves, increasing both

organization and instability, and thus constituting a "running-up" tendency in the universe. This formulation is achieved by the construction of an ecological theory whose logical categories have mathematical interrelations.

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# ATMOSPHERIC MOISTURE IN RELATION TO ECOLOGICAL PROBLEMS

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The appearance in the pages of Ecology during the last several years of a number of papers dealing with the relation of atmospheric moisture and evaporation to ecological problems indicates that ecologists are well aware of the importance of the subject. At the same time, these papers demonstrate that much confusion exists as to the nature of evaporation and the relation between atmospheric humidity and evaporation. Because ecologists continue to expend much effort on the subject, it seems desirable to reopen the discussion.

## Saturation Deficit

In a paper modestly entitled "A Note on Evaporation," Leighly ('37) critically examined the relation of evaporation to ecological problems and attempted to clarify the objectives of ecologists and to resolve their confusion when dealing with this subject. He made special reference to a paper by Anderson ('36).

Anderson advocated the use of vapor pressure deficit (usually called saturation deficit by ecologists) rather than relative humidity in ecological studies. In his introduction he stated (p. 277) correctly that

Evaporation is a dynamic process and represents the net difference between the number of molecules leaving a surface and the number returning to the surface during some unit of time.

However, he completely ignored this physical principle (p. 277) when he said:

Very obviously the importance of atmospheric moisture as a factor affecting the rate of evaporation lies not in the absolute quantity of moisture present but in the relation between the amount present and the amount that could exist under the same conditions without condensation.

Leighly clearly demonstrated that Anderson's analysis and conclusions were un-

tenable. Nevertheless, discussions that have since appeared in the pages of Ecology and elsewhere (Strohecker, '37; Thut, '38; Welton and Wilson, '39) indicate that Leighly's paper either has not been understood or has been ignored.

After pointing out the well-known fact that the net exchange of water molecules between the surface of an evaporating medium and the air is a function of the vapor pressures of the two media, Leighly showed that evaporation is proportional to the vapor pressure gradient between the evaporating surface and the air.

This point may be illustrated by consideration of the following example given by Anderson ('36, p. 278):

Evaporation will therefore occur more rapidly from a moist surface under the same conditions into an atmosphere with a relative humidity of 70 per cent at 80° F. than into an atmosphere with the same relative humidity at 60° F.

As seen in figure 1, the vapor pressure of saturated air at 80° F. is practically twice that of saturated air at 60° F., being 1.0334 and .5220 inches of mercury, respectively. Similarly, at 70 per cent saturation the vapor pressure of the warmer air is approximately twice that of the cooler, being .7234 inches as against .3654 inches. Thus, the saturation deficit in the air at 80° F. is twice that of the air at 60° F., and Anderson maintains that evaporation in the former case will be twice as rapid as in the latter.

Actually, if the evaporating surface is assumed to have the same temperature in both cases, as Anderson does assume, moisture will evaporate into both atmospheres only if the temperature of the evaporating surface is above 69.3° F., at which point its vapor pressure would equal that of the atmosphere 70 per cent saturated at 80° F. If the temperature
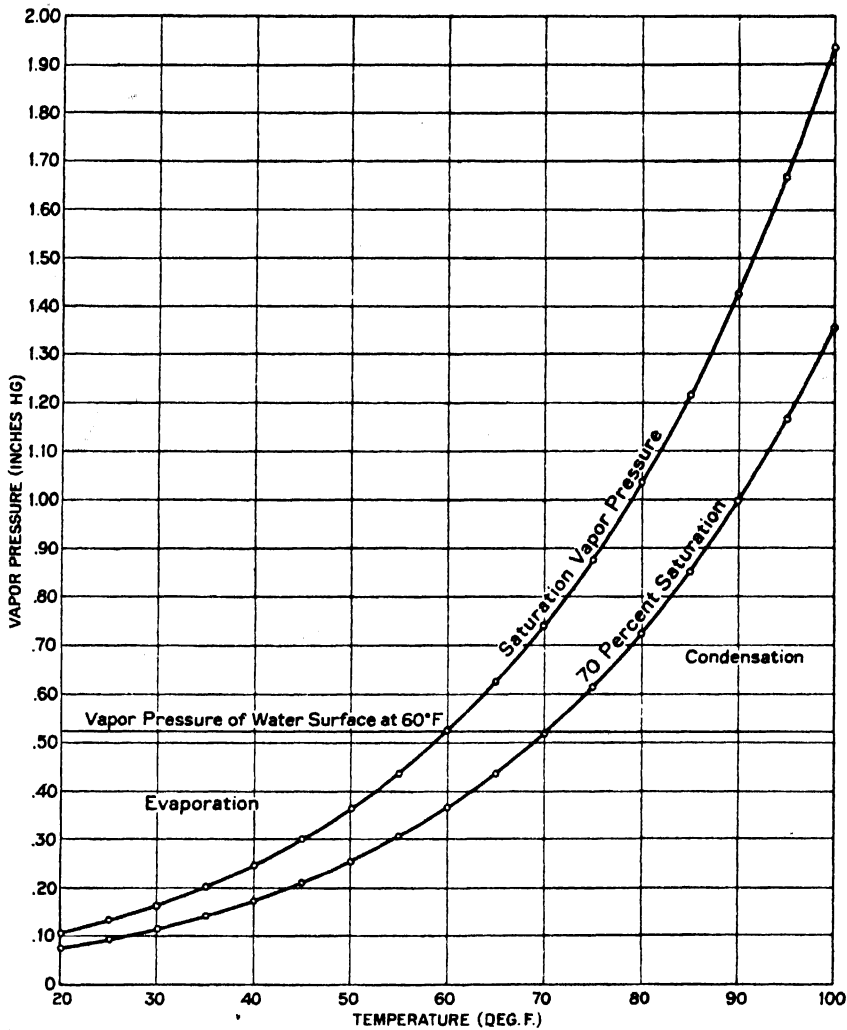
FIG. 1. Vapor pressure in inches of mercury of saturated air and in air at 70 per cent saturation.

of the water surface were 70° F. its vapor pressure would be .7399 inches. Since the vapor pressure of the air 70 per cent saturated at 80° F. is .7234 inches there would be a small gradient and a slight amount of evaporation. At the same time the vapor pressure of the air 70 per cent saturated at 60° F. is only .3654 inches and there would be a large vapor pressure gradient between the water surface and the air and rapid evaporation. If the temperature of the water surface were increased, its vapor pressure would rise and the gradients between the water surface and the two air bodies would rise. The gradient of the cooler

air would remain larger, however, and evaporation into the cooler air would be more rapid.

If the temperature of the water surface were 60° F. there would no longer be evaporation into the atmosphere which is 70 per cent saturated and at 80° F.. but condensation, because the vapor pressure of the air exceeds that of the water surface. The vapor pressure of the water would be .5220 inches and that of the warmer air .7234 inches. Therefore, the molecular energy of the moisture in the air would exceed that of the moisture at the water surface and there would be a net transport of water molecules from

the air to the water, or condensation, not evaporation. On the other hand, the vapor pressure of the cooler air is only .3654 inches, which is less than that of the evaporating surface. In this case, because of the net transport of water molecules from the water to the air, there would be evaporation. If the temperature of the water surface were 80° F., the same as that of the warmer air, its vapor pressure would exceed those of both the warmer and colder air bodies and evaporation would occur into both, but more rapidly into the colder air because of the greater vapor pressure gradient.

Generalizing from figure 1 one may say that whenever the temperature and relative humidity of the air are such that its vapor pressure exceeds that of the evaporating surface there will be condensation. When the vapor pressure is less than that of the evaporating surface there will be evaporation. The portions of the curves above the horizontal line represent conditions producing condensation whereas the portions below represent conditions which bring about evaporation. As the temperature of the air is reduced from 70° F., saturation deficit becomes smaller, but since the vapor pressure gradient between the water surface and the air increases, evaporation will increase. As air temperature increases from 70° F., saturation deficit increases but there will be no evaporation. On the contrary, there will be an increase in condensation as air temperature rises and the vapor pressure gradient between the air and the water surface becomes larger.

In the revised edition of "Plant Ecology," Weaver and Clements ('38, p. 346) used Anderson's example but went even beyond his conclusions when they stated:

But habitats having the same vapor pressure deficits do influence evaporation rates in the same way whether temperatures are identical or not.

That constancy of vapor pressure deficit has no bearing on evaporation rates can be seen in figure 2, where constant vapor pressure deficits of .20 and .40 inches have been plotted. With a vapor pressure deficit of .20 inches and a temperature of the evaporating surface of 60° F., evaporation will occur with increasing rates as the air temperature diminishes below 69.3° F. With air temperatures above 69.3° F., moisture will condense from the air upon the water surface in increasing amounts as air temperature increases. With a constant vapor pressure deficit of .40 inches evaporation into the air will occur at air temperatures below 76.6° F. and condensation upon the water surface at air temperatures above 76.6° F. Increasing the vapor pressure deficit merely increases the temperature at which the shift from evaporation to condensation takes place.

If the vapor pressure of the air exceeds that of the water surface condensation will occur. If the vapor pressure of the water surface exceeds that of the air, evaporation will ensue. Therefore, the direction and size of the vapor pressure gradient, and not vapor pressure deficit, is what determines whether evaporation or condensation will occur and its magnitude.

Vapor pressure deficit would be directly related to evaporation only when the temperatures of the air and of the evaporating surface are equal. If, in Anderson's example, the air at 80° F. and that at 60° F. had been associated with evaporating surfaces of 80° F. and 60° F., respectively, there would have been more evaporation in the former case, not because the vapor pressure deficit is greater but because the gradient between the vapor pressures of the evaporating surface and the air is greater (see figure 1).

Every ecologist knows that it is practically impossible to find in nature equality of temperature between evaporating surface and the air above, and that it is a condition which could be maintained in a laboratory only with great difficulty. Due to the transfer of heat, there is a
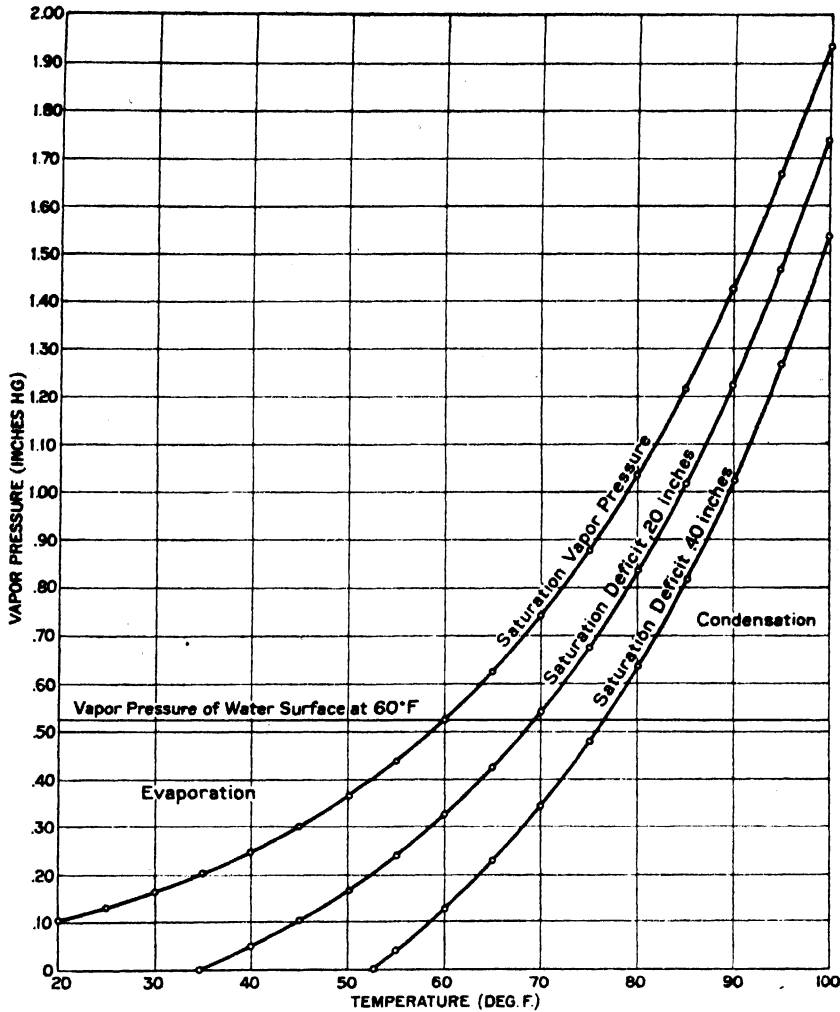
FIG. 2. Vapor pressure in inches of mercury of saturated air and of air with constant saturation deficits of .20 and .40 inches.

tendency toward a temperature equilibrium between the evaporating surface and the overlying air, but such an equilibrium is rarely attained.

To believe that vapor pressure deficit has any influence whatever on the number of molecules leaving an evaporating surface and the number returning to it is as unreasonable as to believe that, for a given pressure of the atmosphere, the mercury column would rise higher in a barometer having a long tube than in one of standard length.

It is entirely possible for evaporation to proceed into saturated air where the saturation deficit is zero. The process is illustrated by water heated on a stove.

In nature it is unimportant and is mentioned here only because it further illustrates that vapor pressure deficit is not directly related to evaporation. Where the temperature of the evaporating surface exceeds that of the overlying saturated air, a vapor pressure gradient will exist and evaporation will occur. Since the moisture condenses immediately the process is highly effective in bringing about a temperature equilibrium, the latent heat of evaporation tending to cool the evaporating surface and the latent heat of condensation tending to heat the air. As soon as temperature equality is established between evaporating surface and saturated air the moisture gradient

will be destroyed and evaporation will cease. Thus, it should be clear that vapor pressure deficit is of no value as an indicator of moisture losses by evaporation or transpiration.

## RELATIVE HUMIDITY

What has been said of vapor pressure deficit is equally applicable to relative humidity. It has been shown above that in two bodies of air both having a relative humidity of 70 per cent with temperatures of 80° F. and 60° F. moisture would be lost by condensation from the first air body and be gained by evaporation into the second, when the evaporating surface has a vapor pressure intermediate between the vapor pressures of the two air bodies, as would be the case if its temperature were 60° F.

There is a diurnal march of relative humidity which accompanies the diurnal march of temperature. On a summer day, with an early morning temperature of 50° F. and a relative humidity of 100 per cent, the vapor pressure of the air would be .3626 inches of mercury. If the temperature of the surface of a water body were also 50° F. the vapor pressures would be the same and there would be no net addition of water molecules either to the air or to the water surface, and consequently neither evaporation nor condensation. As the air temperature rises to 60° F., if moisture is neither added nor abstracted, the vapor pressure will remain at .3626 inches, the relative humidity will drop to 70 per cent, and a vapor pressure deficit of .1594 inches will have developed. As the air temperature rises to 70° F., 80° F., and 90° F., the relative humidity will fall to 49, 35, and 26 per cent, and the vapor pressure deficit will increase to .3743, .6708, and 1.0608 inches, respectively. But, as long as the water temperature remains at 50° F., the vapor pressures of the air and the water surface are the same and there can be no evaporation.

Evaporation will occur only when the vapor pressure of the water surface ex-ceeds that of the air. With a rise in air temperature or with direct absorption of radiant energy, the water temperature will rise and the vapor pressure of the water will become greater than that of the air. When a vapor pressure gradient is thus established, more water molecules are emitted from the water surface than are returned to it and evaporation occurs. Also, the moisture concentration and consequently the vapor pressure of the air may be reduced. As the air increases in temperature, turbulence due to convection may be set up, causing mixture of surface layers with drier air from aloft. Similar dissipation of moisture into the upper levels of the atmosphere may be caused by mechanical turbulence due to wind movements. Wind, therefore, effects evaporation simply through lowering of the vapor pressure of the air in relation to that of the evaporating surface. Generally speaking, the greater the intensity of turbulent mixing, the drier will the surface air become, the larger will be the vapor pressure gradient, and the greater the evaporation.

The foregoing illustrations have been elaborated at length to emphasize the fact that evaporation as a physical process is dependent upon a vapor pressure gradient between the evaporating surface and the air and is not related directly to relative humidity or to vapor pressure deficit in the air.

## OTHER MEASURES OF ATMOSPHERIC MOISTURE

Turnage and Shreve ('39) described an experiment conducted for the purpose of relating evaporation from a porous bulb atmometer to humidity and wind. After commenting on the "complexities involved in attempts to present an index of atmospheric aridity," they state that each of the current expressions of humidity—vapor pressure, relative humidity, dew point, saturation deficit, and wet bulb depression—has its value, but urge that each investigator "publish the direct readings of the psychrometer, the tem-

peratures of the wet and dry bulbs, from which the analytical reader could calculate whatever humidity expression suits his own needs."

It is difficult to see how these expressions of humidity can meet the serious needs of ecologists, since relative humidity and saturation deficit (vapor pressure deficit) have no direct relation to evaporation. Because evaporation occurs only when inequality exists between the vapor pressures of the evaporating surface and the air, it should be apparent that evaporation can never be determined from measurements of vapor pressure of the air alone. Dew point is simply the temperature of saturation of the air; thus, it merely provides a means for determining vapor pressure and cannot be any more useful than vapor pressure in measuring evaporation. Wet bulb depression as an isolated measurement has less utility than any of the other expressions, because without the dry bulb temperature and barometric pressure it is impossible to determine vapor pressure or moisture concentration in the air.

Turnage and Shreve reported that they had found a proportionality between evaporation from an atmometer, at a given wind velocity, and wet-bulb depression. Such proportionality should be expected because an atmometer bulb is in reality a wet bulb. A close relationship would be surprising, however, because of the larger size and much larger heat capacity of the atmometer bulb. Since the authors published only smoothed curves the degree of relationship is not revealed.[1]

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[1] There would necessarily be a variation with temperature in the proportionality between evaporation from an atmometer, at a given wind velocity, and wet-bulb depression. At 0° C., 595.9 calories of heat are required to evaporate one cubic centimeter of water, whereas at 40° C., only 574.0 calories are required. Thus, at low temperatures the evaporation of a given amount of water will bring about a greater cooling and consequently a greater wet-bulb depression than at high temperatures. Probably in ecological studies this source of error can be neglected.

Another procedure frequently employed by ecologists is illustrated in the study by Turnage and Shreve. After evaporation is measured from the atmometer, an attempt is made to find some simple meteorologic function that is proportional to the evaporation. Even though such a proportionality were discovered, it is a fallacy to believe that some simple function of vapor pressure of the air can be used as a datum to which coefficients representing physiological functions can be attached so as to give an expression for transpiration.

## THE EVAPORATING POWER OF THE AIR

The porous bulb atmometer is useful to illustrate the processes of evaporation and transpiration in the class room, but does not provide measurements that can be related to actual transpiration or to evaporation from a free water surface or a land surface. The same is true of data secured from evaporation pans.[2] Both instruments are supposed to supply an index of the *evaporating power of the air,* but this theoretical evaporating power is unrelated to actual evaporation or transpiration.

The amount of water lost by transpiration from an area depends upon the density of plant cover and the character of the plant association as well as upon atmospheric conditions. Transpiration is partly a function of leaf area, which varies seasonally with the growth cycle of the plant. It also depends on water requirements, osmotic values, and the number, nature, size, and behavior of the stomata, which vary from plant to plant and from species to species. None of these factors is represented in pan or atmometer measurements.

Evaporation from the surface of the land is limited to that proportion of the precipitation which is not removed by surface or underground run-off or tran-

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[2] A possible means whereby the porous bulb atmometer may be utilized in an instrument for determining actual water loss from a natural surface is discussed in a later section.

spired by plants. Since run-off is in large measure dependent on the characteristics of the storms which produced the precipitation and on the nature of the land surface, both of which are independent of the evaporating power of the air, it follows that evaporation from the land is largely dependent upon the moisture available for evaporation. When no moisture is available, evaporation is impossible regardless of the so-called "evaporating power" of the air.

It might be expected that evaporation from a free water surface would bear a close relationship to water losses from a pan or an atmometer. However, without a complicated mechanism, involving heating and cooling coils and extremely sensitive controls, it would be impossible to maintain at the surface of the water in the pan a temperature equal to that of the free water surface. With differences of surface temperature the vapor pressures of the two surfaces would be different and consequently there would be variations in evaporation. The walls of a pan, by interrupting the natural air flow, create artificial mixing conditions in the atmosphere, which also result in variation in the evaporation from the two water surfaces.

Whereas hydrologists and engineers have become interested in evaporation largely from the need of determining water losses from lakes and reservoirs, ecologists and agronomists have approached the problem from the standpoint of evaporation from land surfaces, transpiration from vegetation, and the moisture requirements of plants.

Several students, recognizing the futility of trying to determine evaporation or transpiration from measurements of atmospheric humidity or of the evaporating power of the air, have used pots, tanks, and lysimeters, so that plants together with the soil mass in which they are growing may be weighed continuously or at periodic intervals to determine losses of water by evaporation and transpiration. This method creates highly artificial conditions because the walls confine the plant roots and interfere with the normal movement of water in the soil, it is too expensive for use on a wide scale, and involves tremendous sampling errors. Results obtained from pot and lysimeter experiments can be considered only as roughly indicative of evaporation and transpiration from natural surfaces.

ATMOSPHERIC MOISTURE GRADIENTS

Evaporation from any surface could be determined directly from the vapor pressure gradient between the evaporating surface and the air and the coefficient of vapor transfer between them. However, the problem is rendered difficult by the fact that the laws of moisture transfer are different in the laminar and turbulent layers of air. In the boundary or laminar layer, which lies immediately adjacent to the evaporating surface and is usually only a few millimeters thick, moisture is transferred by diffusion alone. In the turbulent layer, however, where eddies bring about vertical motion in the air, vapor is transferred by turbulent interchange.

Leighly ('37) presented a method of measuring evaporation whereby he avoided the turbulent layer entirely and confined his study to the boundary layer where the vapor pressure gradient is linear and where the coefficient of diffusion can be used. However, the making of moisture determinations at two levels and the recognition of vapor pressure differences within a layer as thin as the boundary layer is impossible with existing instruments. Thus, the use of Leighly's method, although it offers great promise in ecological studies, must await the development of more sensitive instruments.

It is likewise possible to determine evaporation and transpiration from any surface by observing the vapor pressure gradient between two levels in the turbulent layer and the intensity of turbulent mixing along this gradient. The mechani-

cal mixing of the air which occurs in the turbulent layer tends to establish an adiabatic distribution of properties of the air, and thus to eliminate differences in moisture concentration. As long as there is no addition to or withdrawal of moisture from either surface of the layer its moisture content will be uniform throughout. If water vapor is emitted from an evaporating surface it will be transported upward and scattered throughout the turbulent layer. Thus, as long as water vapor is flowing upward into the turbulent layer the moisture concentration will be highest at the base and will diminish upward. In this way a moisture gradient is established. Such a gradient owes its existence to the continued addition of moisture from below; when evaporation ceases the moisture will soon be distributed uniformly throughout the turbulent layer and the gradient will be destroyed.

In the same way an abstraction of moisture from the base of the layer by condensation will create a moisture gradient directed downward, which can be maintained only as long as the removal of moisture continues. With a given intensity of mixing in the turbulent layer an increase in the rate of evaporation will result in an increased moisture gradient. In order for a given moisture gradient to persist, the greater the intensity of turbulent mixing the greater will be the required evaporation.

The process of moisture transfer in the atmosphere is analogous to the transfer of heat along a metal rod. Heat applied at one end of a rod will flow along it to the other end. Knowing the temperatures at two places on the rod and the index of conductivity of the metal, it is a simple matter to determine the rate at which heat is applied. When the heat source is removed the temperatures at the two points will soon become equal. It would be impossible to determine the rate of heat application by knowing the temperature at only one point on the rod. It is similarly impossible to determine the rate of emission of moisture from an evapo-

rating surface into the air from observations of moisture concentration at a single point in the atmosphere.

A method of measuring evaporation and transpiration from natural surfaces, based on recent developments in aerodynamic theory and utilizing observations of moisture gradient and the coefficient of mixing in the turbulent layer, has been developed by Thornthwaite and Holzman ('39). The method was described in some detail and the determinations of evaporation and transpiration from a meadow by days for the month of January 1939, as well as by single hours for individual days in the autumn of 1938, were presented.

It should be emphasized that in this method evaporation is actually measured just as stream discharge is measured by using gage heights and current velocity determinations and that errors are due solely to instrumental inaccuracies. The vapor pressure is determined at two levels by means of hygrothermographs. The rate of air transport is determined by the use of two anemometers at these levels.

The method was first tested at the Department of Agriculture experimental farm in Arlington, Virginia. The instruments were set up in October 1938 in a meadow of perennial grasses which had recently been cut, and which remained more or less green throughout the winter. The instruments were mounted in a vertical line 2 feet and 28 feet above the ground.

The hair hygrometer is recognized as being deficient in many respects, but it gives a continuous record and, with careful and frequent calibration in a controlled humidity chamber and by using nonhygroscopic metal charts, reliable results can be obtained. A new type of instrument for determining moisture concentration, which gives a continuous record of dew point temperature, is now being tested and it is hoped that the new dew point recorder will overcome most of the difficulties experienced with existing instruments.

There is a possibility that the porous bulb atmometer may be adapted for use in determining vapor pressure gradients. As mentioned earlier, Turnage and Shreve ('39) have reported finding a proportionality between evaporation from an atmometer at constant wind velocity and wet bulb depression. If the bulb is housed so that it is subjected to a constant air speed, the water loss could be read as average wet bulb depression for the time interval. With average temperature for the same time interval average vapor pressure could be computed. In other words, the atmometer might be used as an integrating wet-bulb. If two such instruments were set up at different heights average vapor pressure gradients might be obtained and used for measuring evaporation and transpiration from a natural surface.

It is not the purpose of this paper to discuss the meteorological or hydrologic implications of the method or to present any of the results which have been obtained. However, the hourly observations for one day are presented in figure 3 for the purpose of illustrating and clarifying many of the points in the foregoing discussion.

The observations given are for a day in early autumn. Between midnight and
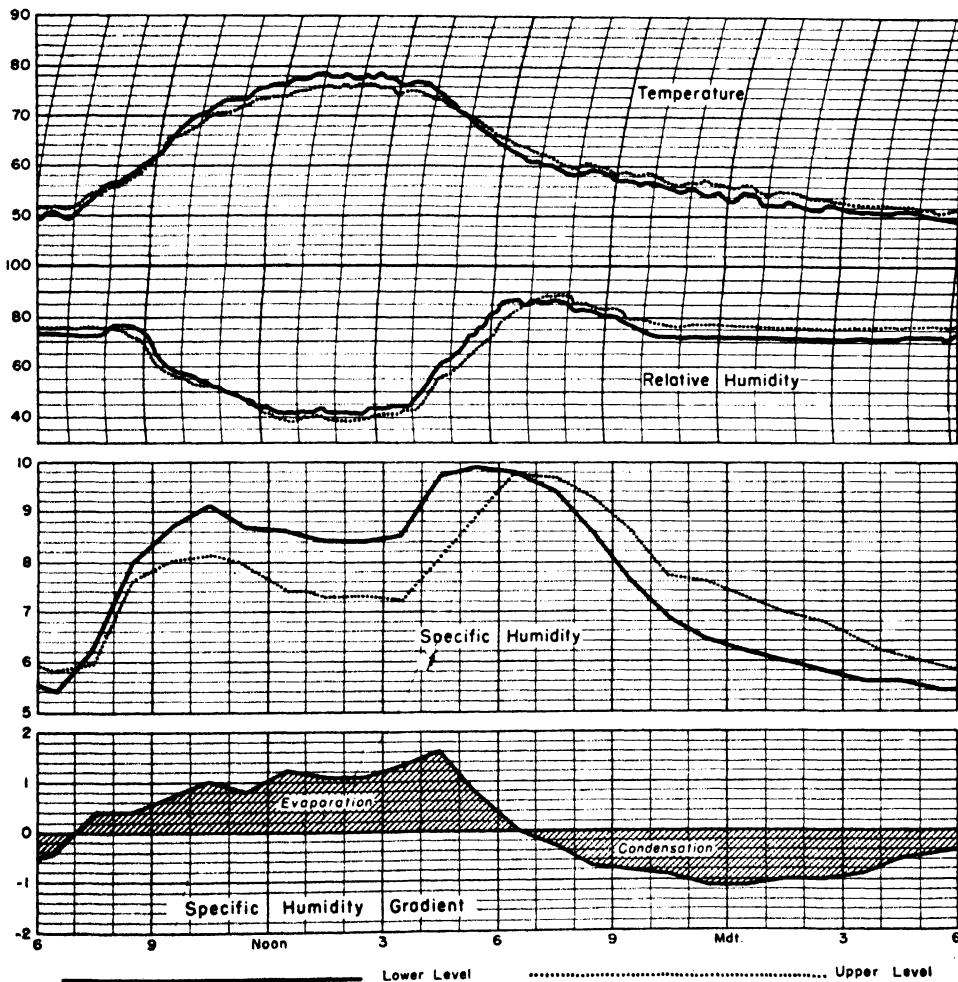


Fig. 3. Temperature and moisture concentration at two levels for the 24-hour period, 6:00 A.M., October 15, to 6:00 A.M., October 16, 1938, Arlington Experimental Farm.

sunrise the specific humidity [3] of the air dropped to a minimum of 5.4 and 5.8 grams in the lower and upper levels due to abstraction of moisture by condensation at the ground level. After sunrise, as the ground temperature increased, water vapor was emitted at an increasing rate and the specific humidity rose rapidly, beginning at the lower level and producing a reversal in the gradient. Shortly before noon the ground had been heated to such an extent that thermal convection commenced and for a time moisture was transported aloft faster than it was being evaporated from the ground and the specific humidity at both levels was reduced about 0.8 grams. About 3:30 in the afternoon, with a diminution of convection, the evaporation again exceeded the rate of transport to the upper air and the specific humidity at both levels rose rapidly and reached the high point of the day about 6:00 P.M. At this time the ground had cooled to such an extent that evaporation had ceased and soon the specific humidity at both levels was identical. As the ground grew colder it acted as a desiccating medium and moisture began to condense out of the air and the specific humidity at both levels diminished throughout the night. The next morning a heavy dew deposit was observed.[4]

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[3] Specific humidity is defined as the mass of water vapor in a given mass of air. In meteorologic usage it is grams of water vapor per kilogram of air. Thus, specific humidity is a measure of the moisture concentration in the air.

[4] Throne ('38) presented a graph on which comparative evaporation, as determined with a dragoyle, at different heights up to 100 feet for three days in early July 1932 was plotted. The observations at different heights were made not simultaneously but in succession during a period of two hours or more, the lowest observations being made first. One series of observations was made in the early afternoon, the others in mid-morning. In all three cases the "comparative evaporation" from the dragoyle increased with height. Neglecting the lack of simultaneity of observations, the results merely indicate that evaporation was taking place from the forest and that a moisture gradient directed upward existed. Had Throne

The procedure described provides not only a measure of evaporation but of condensation as well, which in many parts of the world is an extremely important source of moisture for vegetation. The importance of condensation directly into the soil is particularly great in summer on black soils which, because of their color, have high rates of cooling due to nocturnal radiation. When moisture concentration is high and radiation at a maximum, as much as .05 inches of water could be added to the soil by condensation during a single night (Ramdas, '38).

Along the California coast much non-irrigated land, receiving not more than 10 inches of rainfall annually, is used for crop production and cantaloupes, lima beans, tomatoes, artichokes, and other vegetables are raised successfully. This is possible only because of the moisture which condenses directly into the soil. It is equally true that in such areas the natural vegetation is much less xerophytic than would be the case were this supplementary moisture not available. Thus, ecologists and agronomists should take into consideration condensed vapor which supplements precipitation.

An evaporation station established on the campus of the University of California at Berkeley in May 1939 has shown that during the summer nighttime condensation often exceeds daytime evaporation. The importance of direct absorption of moisture from the air by organic matter has also been demonstrated.

In dealing with the climatic basis of plant distribution a function of moisture must be employed. It is recognized that depth of precipitation is not satisfactory as an index of plant growth. Plant growth is related to the actual moisture used rather than to total precipitation. Moisture available for plants, considered

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made similar observations before sunrise at a time when condensation was occurring he would certainly have found a gradient that decreased with height. The results as obtained by the dragoyle cannot be used to determine the actual evaporation or condensation.

on an areal basis and neglecting ground storage, may be expressed as:

$$I = (P + C) - (R + E)$$

where $I$ is the index of effective precipitation, $P$ is the total precipitation, $C$ is condensation, $R$ is combined surface and ground water run-off, and $E$ is evaporation. Means for the adequate measurement of precipitation and run-off are already available, but the measurement of condensation and evaporation has not previously been possible.

## PRECIPITATION EFFECTIVENESS INDICES

It was the inability to determine precipitation effectiveness directly that led to the development of the many empirical formulae for expressing the effectiveness of precipitation. Transeau ('05), one of the earliest to be concerned with the problem, used the quotient of total annual measured precipitation divided by evaporation as computed by Russell ('88) for a period of 12 months in 1887 and 1888 for about 150 stations. Lang's ('20, pp. 107–123) "rain factor," de Martonne's ('26) "index of aridity," Meyer's ('26) "N–S quotient,"[5] and the studies of Emberger ('30) and Falkner ('38) represent other attempts to determine effective precipitation. The climatic classifications of Köppen ('00; '23) and Thornthwaite ('31; '33) both employ formulae for determining the effectiveness of precipitation. These studies, and all others like them, are empirical and are unsatisfactory for determining directly the moisture relations of plants. Only when measurements of evaporation and condensation from natural surfaces under

different types of plant cover are available for a large number of locations throughout the country will it be possible to evaluate the moisture factor in plant distribution.

## SUMMARY

The problem of atmospheric moisture in relation to ecological problems is still far from being solved. When ecologists acquire a basic understanding of the process of moisture transfer between the land surface with its vegetation and the atmosphere, the inadequacy of present measurements of atmospheric moisture and the futility of attempting to determine relationships between simple functions of atmospheric moisture and physiological functions of plants will become apparent. Empirical indices of precipitation effectiveness are useful but necessarily have great limitations. The direct measurement of emission of water from natural surfaces into the air is feasible but before it can be undertaken on a large scale more satisfactory instruments for measuring the moisture concentration of the air must be devised. Nevertheless it is only when measurements of evaporation and condensation from natural surfaces under different types of plant cover are available for a large number of locations throughout the country that it will be possible to evaluate the moisture factor in plant distribution.

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[5] Meyer's N–S (Niederschlag-Sattegungsdefizit) quotient is obtained by dividing precipitation by saturation deficit. Since saturation deficit is employed in the Meyer ratio, it has become popular with a number of ecologists. Actually the Meyer ratio is subject to the same criticism as is saturation deficit alone, and as a general climatic index it is more difficult to compute, requires more varied meteorological observations, and is in the end less satisfactory than a number of other indices.

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# AN EXPERIMENTAL STUDY OF CERTAIN EFFECTS OF TEMPERATURE ON DIFFERENTIAL GROWTH OF PULLETS [1]

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Hesse ('21) gave a comprehensive survey of the relations between the weight of the vertebrate heart, both absolute and relative, and total body weight. He listed in detail an impressive collection of data from mammals and birds killed in nature which show that, other things being equal, the hearts of these warm-blooded animals from colder regions are proportionately heavier than are those of related forms from warmer habitats. For example, birds from the tundra which are winter residents in Germany, have hearts with a greater relative weight than similar birds which are more permanent residents in the same area. This extensive paper, which is summarized in a paragraph by Hesse, Allee and Schmidt ('37, p. 392), stimulated the following experimentation.

## MATERIAL AND METHODS

In connection with other studies, we were growing white leghorn chicks in batteries. The adequacy of our treatment is shown by the fact that after the early death of one of the 25 day-old chicks received on September 19, 1938, there were no other deaths until we began terminating the present experiment. At that time one pullet in the cold room died of injuries inflicted by its battery mates. Otherwise all the chickens were healthy when killed and were of excellent flavor when eaten.

The baby chicks were reared in a well ventilated dark room and were given twelve hours of illumination per day. Light was furnished by an ordinary 60-watt bulb which was controlled by a time switch and was supplemented, during the lighted period, by irradiation from a lamp relatively rich in ultra-violet rays. The

room temperature was held between 21° and 24.5° C. by an ordinary room thermostat. The chicks were given additional heat in a simple brooder until they were four weeks old. At that time they were placed in wire walled battery pens that measured 34 × 36 × 16 inches; six chicks were kept in a pen. Those which were used as controls remained in these batteries and at this room temperature until they were sacrificed.

At 63 days of age, six of the pullets were selected at random and placed in a pen that measured 26 × 20 × 23 inches which was housed in a large cold room with a temperature of 6° C. Ventilation in this room was imperfect since it depended on the somewhat infrequent opening of the heavy door. No attempt was made to control humidity in either room. Both flocks were given similar food and food and water stood before them at all times. Both were equally illuminated with approximately the same quantity and quality of light. Temperature and associated changes in relative humidity were the only differences of major importance.

After 109 days in the cold room, the pullet, whose death was mentioned previously, was seriously pecked by its fellows. This event determined the beginning of the end of the experiment. The other birds in this flock were killed between the 115th and the 123rd days of exposure to cold. The birds were weighed each week during their entire laboratory life; hence it was easy to select from the fifteen pullets held at room temperature, one which was approximately equal in weight to each individual from the cold room. These birds, selected only because of being approximately equal in weight, were treated for statistical purposes as paired controls. They were killed between the 110th and

TABLE I. *Total weight in grams and percentage of growth*

| Individual | Cold room | | | Individual | Warm room | | |
|---|---|---|---|---|---|---|---|
| | 63 days | 172–186 days | % gained | | 63 days | 173–188 days | % gained |
| BG | 510 | 2170 | 76.50 | PY | 720 | 1930 | 62.69 |
| GG | 490 | 1400 | 65.00 | GG | 565 | 1440 | 60.21 |
| PG | 540 | 1830 | 70.49 | BR | 720 | 1790 | 59.78 |
| BY | 510 | 1390 | 63.31 | BP | 620 | 1330 | 53.38 |
| RY | 535 | 1440 | 62.85 | RR | 635 | 1490 | 57.38 |
| YY | 555 | 1550 | 64.19 | YY | 600 | 1590 | 62.26 |
| Mean | 523.3 | 1630 | 67.06 | | 643.3 | 1591.7 | 59.28 |

the 125th day after their six fellows were placed in the cold room and averaged three days older. All the pullets in this experiment were between 173 and 188 days old when killed.

Various measurements and weights were taken at the time of autopsy. These will be analyzed with the aid of a short series of tables, the first of which (Table I) shows total weight in grams of each pullet at the time of constitution of the flock in the cold room and at the end of the experiment.

When the young pullets were placed in the cold room they averaged 120 grams lighter than the birds which were later selected as their paired controls because they had approximately equivalent weights. The difference of 120 grams is statistically significant with $P = 0.0058$.[2] During the following period of almost four months, those at the lower temperature grew more rapidly and showed a mean gain of 67.06 per cent of their final body weight as compared with a similar mean gain of 59.28 per cent for the pullets at the higher temperatures. The difference of 7.78 per cent is also statistically significant with $P = 0.0078$. The smaller initial weight followed by more

[2] Statistical significance was calculated by Student's method for paired comparison of small samples. $P = 0.05$ is the same as twice the standard error or three times the probable error. This is frequently regarded as marking the upper limit of statistical significance. The lower value of $P$, the smaller the probability of obtaining similar results by random sampling and hence the higher degree of significance. $P = 0.0058$ indicates good validity in the statistical sense.

rapid growth of the pullets in the cold room resulted in young fowls which were somewhat but not significantly heavier than their controls.

Kleiber and Daugherty ('34) report that baby chicks kept in groups of five at environmental temperatures of 21°, 27°, 32°, 38°, and 40° C. during the period of six to fifteen days of age, grew more rapidly with decreasing temperature. These results are in keeping with our findings even though they are based on such different ages and temperature levels as to be scarcely comparable.

The other available data are summarized in tables II and III each line of which is a condensation of data such as are given in detail in table I. In certain indicated instances fewer than six comparisons were possible otherwise each summary is based on the amount of data shown in table I; the first two lines directly summarize those data.

The result of weighing the skin and feathers immediately after their removal departed from expectation. It was only when considered in the light of the information gained by the measurements to be recorded in table III that an explanation for the lack of significant difference between the two flocks became apparent. Further discussion of this point will be deferred for the present.

The heart was removed by cutting at the base of the large blood vessels. The blood was squeezed out. The weight given is for the empty heart still surrounded by the pericardium from which, however, all fat had been removed. The hearts from pullets which had spent ap-

TABLE II.  *Differences in weight in grams of birds reared at low and high temperatures*

| Comparison | 6° | 21°–24.5° | Difference | P |
|---|---|---|---|---|
| Body weight | 1630.0 | 1591.7 | 38.3 | 0.41 |
| % gained | 67.06 | 59.28 | 7.78 | 0.0078 |
| Weight of skin and feathers* | 198.08 | 196.72 | 1.36 | 0.925 |
| Weight of heart | 10.63 | 7.41 | 3.22 | 0.007 |
| $\dfrac{\text{Weight of heart}}{\text{Total weight}}$ | 6.52°/$_{00}$ | 4.59°/$_{00}$ | 1.93 | 0.012 |
| $\dfrac{\text{Weight of heart}}{\text{Weight of skinned birds}}$ | 7.09°/$_{00}$ | 5.09°/$_{00}$ | 2.00 | 0.044 |

\* Five paired comparisons.

proximately four months in the cold room averaged 3.22 grams heavier than their paired controls with $P = 0.007$. Since the two flocks of pullets were of approximately the same weight, this means that the hearts from the cold room represented a somewhat greater proportion of the total body weight. Calculated in terms of *per mille* this amounted to 6.52°/$_{00}$ as contrasted with 4.59°/$_{00}$ for those from the higher temperature. The difference of 1.93°/$_{00}$ has a $P$ value of 0.012 and is plainly significant. When considered in relation to the weight of the skinned birds, the relative proportions were 7.09°/$_{00}$ and 5.09°/$_{00}$ respectively. This difference of 2.00°/$_{00}$ is less significant statistically but still has a $P$ value of 0.044.

These experimental results support Hesse's findings from birds in nature ('21) in that the hearts of these pullets from the cold room were absolutely and relatively heavier than were their controls of the same stock and age which differed only in that they had been reared at a higher temperature.

In addition to the items shown in table II, the adrenals, thyroids, ovaries, and oviducts were removed and weighed when fresh. The first two showed no indication of a differing trend in weight; the ovaries and oviducts had a tendency to be heavier at the lower temperature. There was, however, much variation and the differences were not statistically significant.

Certain measurements were also taken; these are summarized in table III. All the measurements except total body length were made with calipers. Those on the heart were taken when that organ was relaxed. Both dimensions were measured at their maximum which means that the width was taken at the base of the auricles. These measurements of the heart support those already presented on the weight of that organ although the observed difference in width is not statistically significant.

TABLE III.  *Measurements in millimeters of birds reared at low and at high temperatures*

| Comparison | 6° | 21°–24.5° | Difference | P |
|---|---|---|---|---|
| Length of heart | 44.68 | 37.90 | 6.78 | 0.034 |
| Width of heart | 28.37 | 26.32 | 2.05 | 0.132 |
| Length plus width | 73.05 | 64.22 | 8.83 | 0.043 |
| Length of body | 394.50 | 417.00 | 22.50 | 0.013 |
| Length of tarsus | 93.78 | 97.52 | 3.74 | 0.004 |
| Length of wing | 24.77 | 25.12 | 0.35 | 0.321 |
| Length of tail* | 17.25 | 19.63 | 2.38 | 0.014 |

\* Four unpaired comparisons calculated according to an appropriate modification of Student's simplest formula.

The other measurements were made according to the directions of Chapman (1934, p. xxv). The total length was not listed in table III since the tails of two in each flock were imperfect. Length of body as used means the length of the specimen lying on its back and measured from the point of the bill to the insertion of the middle tail feathers. The length of tail was taken from the insertion of the middle tail feathers to the end of the

longest feather. The length of tarsus was measured from the insertion of the middle toe to the proximal end of the tarsus. The length of wing means the distance from the so-called bend of the wing to the end of the longest primary feather.

Contrary to the situation shown by measurements and weights of the heart, these values are greater for the pullets which had been reared at room temperature than for those from the cold room. The difference of 0.35 mm. in length of wing was not significant; the others were clearly so.

## DISCUSSION

The data just summarized show that for these white leghorn pullets the body, wings, and tail were longer when the individuals had been reared at relatively high room temperatures while the heart was actually and relatively larger in those reared at 6° C. The skin and feathers of the two flocks had approximately similar weight. We are now in a position to consider the possible reasons for this equality. The birds from the cold room were shorter in proportion to their weight; that is, they were more stocky individuals and had less surface (skin) per unit of weight than their controls from the higher temperatures. The latter had also definitely longer and presumably heavier tail feathers. These items balanced any tendency toward increase in weight of skin and feathers from the birds in the cold room and produced an approximate equality so far as our small flock is concerned.

The observed differential in body proportions is in keeping with the well-known principle of Bergmann (Hesse, Allee and Schmidt, '37, p. 385) that animals from northern climates tend to be larger in size and have less surface in proportion to body weight than their southern relatives. This relationship has usually been interpreted in relation to heat conservation.

These data also support the principle of Allen ('77) of a "marked tendency to enlargement of peripheral parts under high

temperature or toward the tropics" which is also discussed by Hesse, Allee and Schmidt. Allen based his generalization on measurement of animals killed in nature. His conclusions have recently been amply confirmed by Rensch ('36) using similar material. Exceptions occur and may be illustrated by Sumner's ('32) observations on *Peromyscus* collected in nature in and near California which show exactly the reverse of the relations called for by Allen's principle.

The results of Sumner's ('09, '15) experimentation, on the other hand, support the rule. In 1915 he summarized his work upon the effect of temperature on the growth of white mice as follows: "Throughout these experiments, I have found differences between the mean measurements of lots which were reared in the cold room and ones which were reared in the warm room. As regards two parts, the tail and the foot, these differences were considerable in amount, and of absolutely certain statistical significance. They were always in favor of the warm-room animals, and were evident in all of my four independent series of experiments." A similar tendency with regard to size of external ear was not constant in occurrence and was of doubtful statistical validity.

Ogle ('34), using white mice, also found that the tails of those reared at 88–92° F. were longer than those of members of the same strain reared at 60–68° F. Those from the lower temperatures had longer and stockier bodies so that they were decidedly heavier animals.

Our results extend this experimental treatment to the domestic fowl but add nothing that is essentially new. The new aspect of our work, so far as we know, is found in the experimental demonstration of the larger size of the heart, both absolute and relative, in pullets reared at low temperatures. This result is according to expectation when considered in connection with the naturalistic observations of Hesse ('21); it is of interest that a change of this kind can be demonstrated

with high statistical probability on so few specimens.

The problem is now open for more thoroughgoing investigation of the various aspects involved. The problems on which light is needed include among others, the duration of exposure which will yield detectible results; the permanence of effects in birds returned to normal conditions; the age at which environmental induction can most readily be produced and whether comparable results can be produced at all in fully mature birds. It would also be of interest to explore experimentally with birds the differential growth responses which illustrate the Bergmann and the Allen effect.

The present experimental treatment does not permit a more exact explanation of the observed differential increase in size of heart with low temperature than did the naturalistic data which were previously available. It still seems that the additional work imposed on the heart by the added labor of maintaining peripheral temperatures under increased cold is probably the causal factor (cf. Hesse, '21).

## SUMMARY

The temperature at which pullets are reared evidently plays a rôle in determining certain morphological features. The birds which were kept at 6° C. during their third to sixth months of age inclusive were shorter in body length, gained more weight, had shorter tarsi and tails and larger hearts than their former flock mates which were kept throughout at 21° to 24.5° C.

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# CLASSIFICATION OF GLEY SOILS FOR THE PURPOSE OF FOREST MANAGEMENT AND REFORESTATION [1]

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## INTRODUCTION

The degree of soil drainage is determined by the depth of the ground water table, or the upper limits of the waterlogged soil layer. Anaerobiosis and hydrolysis, dominating the strata of soil below the ground water table, produce a deoxidized, often highly dispersed, sticky zone, mottled with reduced oxides of iron, and called gley horizon (Wyssotzky, '05). At a certain depth the gley horizon is underlain by an impervious substratum, called "dead horizon of dryness" (Wyssotzky, '30). Soils in which the gley layer occurs within the reach of the root systems of trees or cultivated plants, *i.e.* at an approximate depth of 7 feet or less, are classified as gley soils. "Hydromorphous soils" and "poorly drained soils" are the other terms applied to the soils of this group.

The process of gleyization may be superimposed upon any member of the great soil groups of the world. The resulting varieties are referred to as gley podzols, swamp podzols, gley laterites, vlei soils, meadow soils, lowland prairie soils, ferruginous soils of mountain valleys, marl soils, etc.

Ordinarily, gley soils occur sporadically, being confined to depressions and areas underlain by impervious substrata. However, in certain regions of America, northern Europe, Siberia and Africa, gley soils are a dominating type occupying hundreds of thousands of acres. The

wide belt of gley soils extending from southern Illinois along the Mississippi River to the flatwoods of Louisiana may serve as an example in the United States.

With the exception of localities with a fairly deep ground water table and areas artificially drained, gley soils are, by and large, forest soils; silviculture is often the most economical and the most sound solution of the problem of their utilization (Krüdener, '16). Nevertheless, forestry as well as farming, may encounter serious difficulties on these soils unless their nature is thoroughly understood.

One of the most detailed morphological studies of gley soils was completed by Zavalishin and Pronevich ('28) as a part of a reconnaissance survey of Pashe-Kapecky forest conducted under Glinka's direction. Among the types of poorly drained soils the authors recognized peat podzol, gley podzolic peat soil, swamp podzol, gley podzol, podzolic gley soil, podzolic gley soil with a deep gley horizon, peat gley soils, and swamp peat soils. These and similar terms have significance in the morphological nomenclature of soil genesis, but they are too long and confusing to be successfully used in practical work. Moreover, they have no direct bearing upon the productivity of soil, particularly forest soils.

In this paper an attempt is made to establish a simple classification of gley soils that would satisfy the needs of silvicultural practice as regards the choice of species, possibilities of natural regeneration, and technique of tree planting.

## EFFECT OF GLEY HORIZON UPON FOREST GROWTH, AND PROPOSED CLASSIFICATION OF GLEY SOILS

Deficiency of air and presence of toxic reduced compounds as a rule prohibit the development of roots in gley layers (Büs-

34

gen and Münch, '29; Woodroof, '33; Heyward, '33; Rigg and Harrar, '31).[8] Therefore, the distance of the gley horizon from the surface controls not only the accessibility of ground water, but also the extent of root penetration and depth of well aerated soil containing available nutrients. These factors in turn determine the type of forest stand, its rate of growth, percentage of cull material, composition of ground cover, vigor of competing vegetation, possibilities of natural reproduction, and stability of stands against the wind (Wilde, '29).

Considering the depth and position of the gley layer in relation to the occurrence of the A, B and C horizons of a mature forest soil profile, the following three types of gley soils may be recognized:

*Alpha gley soils* or *shallow gley soils,* that is semiswamp, more or less permanently wet soils [4] with a shallow gley layer grading into the $A_2$ or $A_1$ horizon.

*Beta gley soils* or *mid gley soils, i.e.* insufficiently drained, periodically wet soils with gley layer superimposed upon the B horizon.

*Gamma gley soils* or *deep gley soils, i.e.* sufficiently drained but rather moist soils with a deep gley layer occurring in the C horizon.

The soils in which the gley layer contacts a purely organic layer $A_0$, *i.e.* peat and muck, present no difficulties in their ecological classification and are not considered in this paper.

The relative position of the gley horizon in the above mentioned types of soil is indicated in figure 1.

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[8] Bald cypress, pitch pine and several other species are known to be exceptions (Adamson, '10; Hesselman, '10; McQuilkin, '35).

[4] The classification of soils into "arid," "dry," "slightly moist," "moist" and "wet" (trocken, frisch, feucht, nassfeucht, nass; Krüdener, '27) is subject to several criticisms. The content of soil moisture varies greatly with the season. The terms "dry," "moist," etc., are purely empirical. The periodical deficiency of moisture in certain types of hydromorphous soils is of greater ecological importance than their maximum saturation.
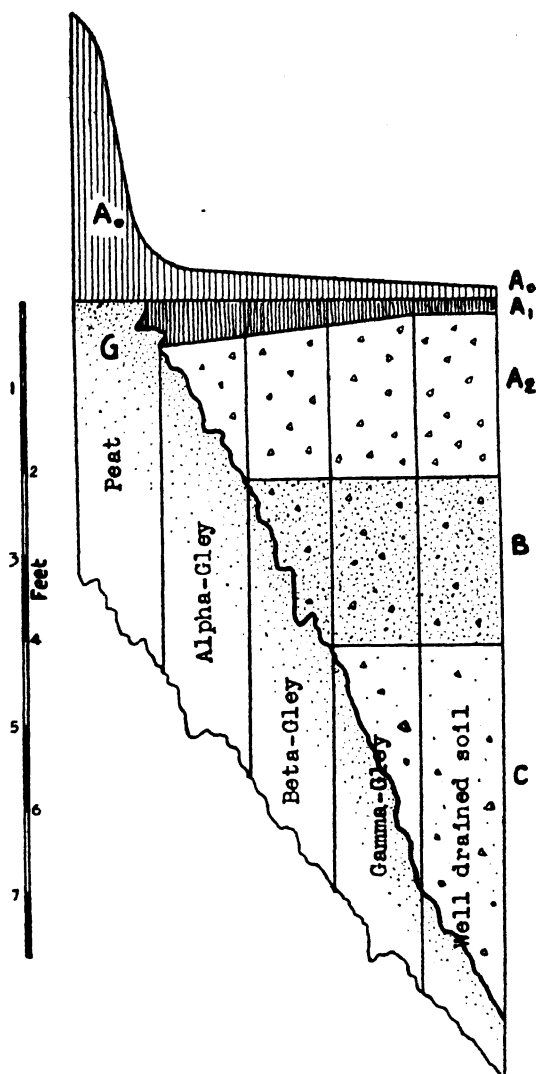


FIG. 1. The position of the gley horizon in different types of soil.

## SILVICULTURAL CHARACTERISTICS OF GLEY SOILS

*Alpha Gley Soils* (Shallow gley soils). —The gley layer protrudes up through the leached horizon, and may reach the horizon with incorporated humus, being thus within about 1 foot of the surface.[5] The influence of the ground water often masks in this type all the other genetical features of the soil profile. Alluvial stream-bottom soils, soils of semi-swamp

[5] The depth of the gley horizon maintains the same ecological significance regardless of whether soil is or is not differentiated into distinct A, B and C horizons.

flats of lacustrine clays or highly colloidal weathered drifts of early glaciations, and various swamp-border soils belong to this group.

The forest cover of alpha gley soils is composed of a rather limited number of species which can tolerate deficiency of aeration. Spruce, balsam fir, cedars, tamarack, bald cypress, pitch pine, black ash, elm, some oaks, cottonwood, and tupelo gum may be quoted as typical representatives. The stands are of a very low productivity and have a high percentage of cull material (fig. 2). The density
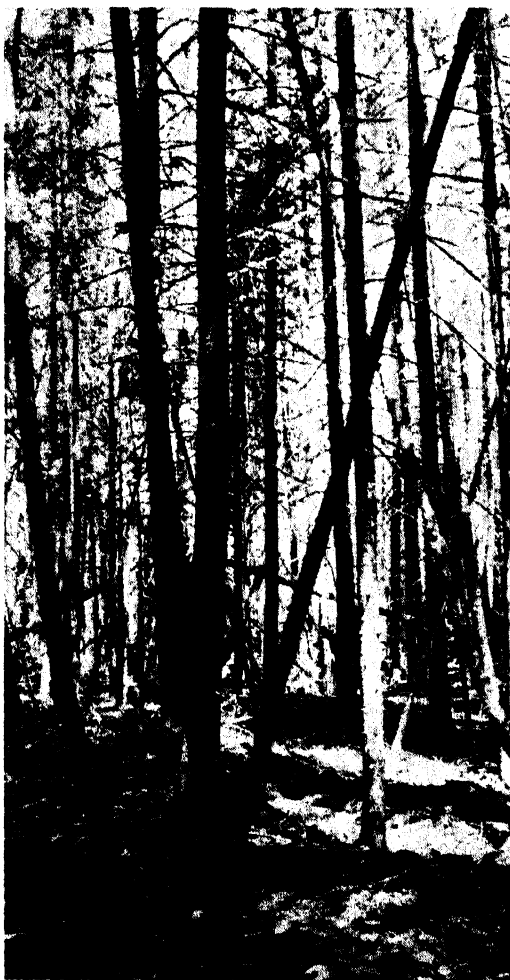


Fig. 2. Interior of a balsam fir and white spruce stand on alpha-gley podzol. Note the superficial root systems and negligible resistance of stand to windfall. Douglas County, Wisconsin.

of the main stand often does not exceed 50 per cent. The ground vegetation is of a distinctly hydrophytic nature including *Polytrichum*, *Sphagnum*, other mosses, sedges, horsetails, bunchberry, some orchids, and often members of the heath family.

The planting of trees on these soils without artificial drainage is not practicable. On the other hand, selective cuttings require a great deal of caution and skill. Usually the condition of the stand on these soils calls for a heavy cutting in order to eliminate infected trees and inferior or unsuitable hardwood species. However, a heavy logging may raise the ground water level and further increase the content of soil moisture due to the larger amount of precipitation reaching the ground and to the reduced transpiration. In places, heavy cuttings on these soils have encouraged the invasion of *Sphagnum* and led to the development of true swamps (Tiurin, et al., '35). The more humid the climate, the greater is the danger of such a conversion. Consequently, alpha gley soils of podzolic or lateritic nature deserve particularly careful handling. Observations of vegetation and humus on cutover lands or windfall areas may serve as a valuable guide to the establishment of a proper cutting intensity.

Alpha gley soils are about the only type where inexpensive drainage may give, under present conditions, some financial return through an increase in productivity of forest stands.

The detection of alpha gley soils presents no difficulties in nature. The attempts to use unsuitable methods of tree planting or selective cutting result in immediate and complete failure on these soils. However, such attempts are rather rare since the adverse effects on these soils are well known to foresters.

*Beta Gley Soils* (Mid gley soils).—The gley horizon occurs immediately below the accumulative layer and sometimes grades into the latter, thus being at a depth of 2 to 3 feet from the surface.

Percolating water and ground water contribute equally to the morphology of these soils. The soils of lower slopes in the mountains, shallow outwash or residual soils underlain by impervious strata of weathered shale or boulder clay, borders of lowland prairie soils in transitional prairie-forest regions, some red and yellow soils underlain by hardpan, and podzols of heavy texture with highly colloidal, accumulative layers are typical examples of beta gley soils.

In the summer period, the surface layers of these soils are usually dry. However, in the fall and particularly in the spring, the water saturates the entire planting layer. An examination of open trenches or at least borings with an auger to a minimum depth of 3 feet may be necessary to reveal the presence of the typical "mottling" of the gley horizon and the true nature of these soils.

Being a transition, this type of soil offers a suitable site for the survival of both upland and lowland forest trees, even if it does not assure their successful growth. Consequently, the forest cover is composed of numerous species, both conifers and hardwoods. A "hardwood coniferous type" was the name usually applied by timber cruisers of early days in northern Michigan and Wisconsin to describe this soil-forest unit. The ground cover association is composed either of mesophytic or saprophytic "raw humus" plants with characteristic mosaic of hydrophytic species, such as bedstraw, bugle weed, Jack-in-the-pulpit, enchanter's nightshade, cranesbill, star flower, horsetail and numerous species of ferns. Shrub thickets are also indicative of this type. With a certain amount of local experience, the ground cover flora may serve as a valuable guide in the survey of these soils.

The productivity and the stability of forest stands on beta gley soils is hindered by a number of adverse conditions. The roots of the trees are confined to a comparatively shallow surface layer of well aerated soil. As a result, the supply of available nutrients is limited. Periodic wetness and the effect of early and late frosts shorten greatly the length of the growing season. Upland species suffer in spring and fall from deficiency of aeration, whereas lowland species suffer and sometimes perish in the summer from drouth. The abundance of weakened specimens encourages the development of parasitic organisms, which contribute to the general decadence of the stand.

Artificial reforestation may require the use of expensive mound or furrow-top planting. Hole plantings are often subject to "freezing out" or "heaving" of seedlings. The deficiency of aeration during the first few years of growth may induce the gradual degeneration of seedlings planted in holes.

Since the stands on beta gley soils may serve as breeding centers for parasites, careful sanitation, i.e. removal of deteriorating material is the chief objective in silvicultural cuttings. On soils of podzolic nature, tending to promote an accumulation of raw humus, there may be a need for partial cuttings of considerable intensity. The group selection method or a suitable modification of Wagner ('15) and Eberhardt ('22) shelterwood strip cuttings should preferably be employed because of the shallow root systems and danger of windfall. On soils of the brownearth group with mull-like floor, the timber should be removed as much as possible without a breaking of the canopy and encouragement of shrubs and weed species. As a general rule, the maintenance of both merchantable conifers and soil-conserving hardwoods in about equal proportion is highly desirable because of the limited supply of available nutrients in the shallow soil layer.

Intercepting ditches, simple vertical tiles, or dynamiting of the impervious interlayers may be found profitable under certain circumstances.

The beta gley soils are not readily discernible, especially in dry summer periods. The failures to recognize them are quite common and often lead to far-reaching

and incurable silvicultural mistakes. A knowledge of this type of hydromorphous soils is of the greatest importance to the forester.

*Gamma Gley Soils* (Deep gley soils.)— The gley horizon reaches its full development in a deeper part of the parent material, usually at a depth of from 5 to 7 feet. However, slight mottling may occur in the proximity of the B horizon, at a depth of about 4 feet. The development of mull humus is often characteristic of gamma gley soils. In all other respects, the composition of the soil profile is but slightly influenced by the ground water.

The roots of the trees develop in a sufficiently deep well aerated and potentially nutritive layer of soil, and receive some additional moisture from the ground water. Of great importance is the relatively negligible seasonal fluctuation of a deep ground water table, which is protected from evaporation by a substantial mantle of soil. Such a fortunate combination of conditions usually leads to an exceptionally rapid growth of timber as well as general stability of forest stands. The composition of stands does not differ conspicuously from those growing on true upland soils. However, the presence of a deep gley layer, is usually responsible for the occurrence of more exacting species than are ordinarily found in a given region on upland soils of similar texture. In this manner, gamma gley soils may cause some confusion in attempts to correlate the distribution of vegetation with the textural properties of soils (fig. 3). The presence of some mesophytic ground cover plants on sandy soils, or hydrophytic plants on heavy soils is another manifestation of the deep gley horizon.

The technique of planting and logging on gamma gley soils requires certain deviations from the normal practices because of a more vigorous growth of inferior associate species, shrubs, and especially sprouts, the roots of which greatly benefit from the ground water. The selection of species for reforestation of ex-
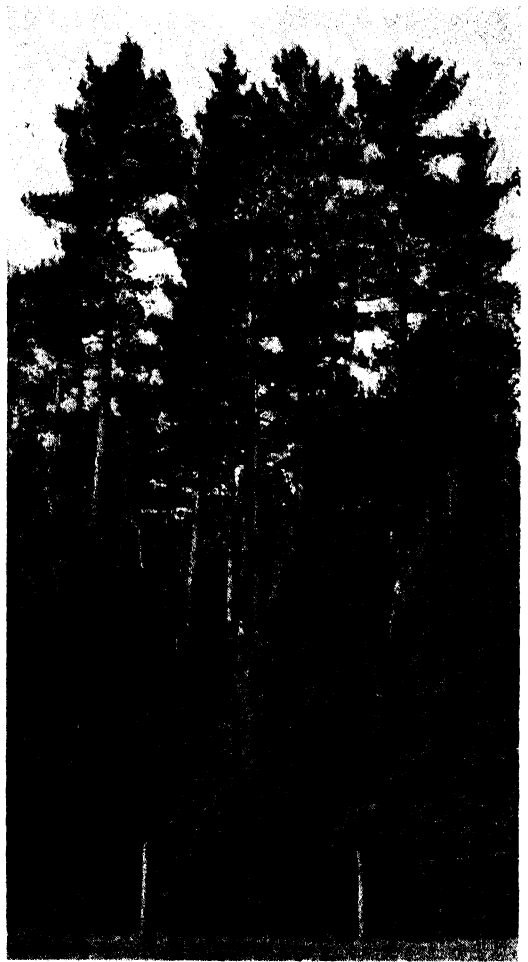


FIG. 3. Highly productive mixture of white and red pine with understory of white spruce and balsam fir on gamma-gley soil of a light sandy texture. Sawyer County, Wisconsin.

tensive cutover lands should be the same as that for well drained soils, since it may take a number of years before the roots of planted seedlings reach the capillary moisture of the deep gley layer. However, in under-plantings or reforestation of smaller protected areas with reduced danger of drouth, more exacting species could be advantageously used to increase the merchantable value of the stand.

A skillful damming of the streams and creation of artificial water basins, may give an appropriate rise to ground water level and result in the development of gamma gley soils.

The nature of gamma gley soils can only be revealed by the use of a long extension
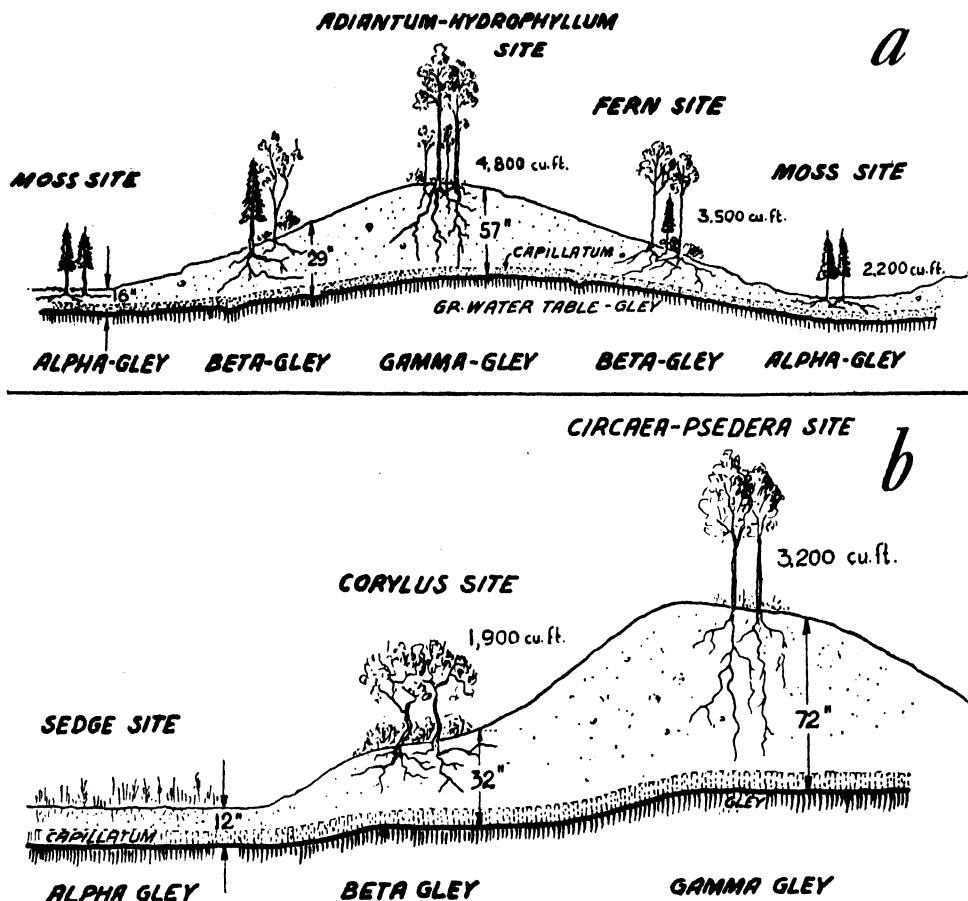
Fig. 4. Effect of gley horizon upon forest growth. (a) Granitic drift of old pre-Wisconsin glaciation in podzol region of northern Wisconsin (Colby series). (b) Calcareous drift of recent Wisconsin glaciation in prairie-forest region of southern Wisconsin (Miami series).

auger or by investigation of deep profile pits. Consequently, these soils are often confused with so-called "well-drained" soils.[6] Forestry suffered considerable losses because of the failure to realize the full potentiality of gamma gley soils. Still greater losses were encountered because the successful growth of certain species on gamma gley soils encouraged the planting of the same species on texturally similar soils with inaccessible ground water. Failure or stagnation of numerous spruce plantations in central Europe is a direct result of insufficient knowledge of ground water conditions.

Two examples of correlation of gley soils with forest growth, as observed in Wisconsin by Wilde ('34) and White ('39), are presented in figures 4a, 4b and 5 and table I. A classical example of correlation of the pine and spruce stands with the ground water level may be found in Krüdener's ('16) work on Russian forests.[7]

[6] Speaking of soil drainage, it seems more appropriate to use three main distinctions "insufficiently" or "poorly drained soils," "sufficiently" or "well drained soils" and "excessively drained" soils. The expression "well drained" covering at present highly productive soils with available "capillatum" (Wyssotsky, '27) and moisture deficient soils with inaccessible ground water is rather unsuitable and misleading.

[7] It should be emphasized that the reaction of vegetation to a certain depth of gley horizon is considerably influenced by the climatic conditions of the region, particularly air humidity.
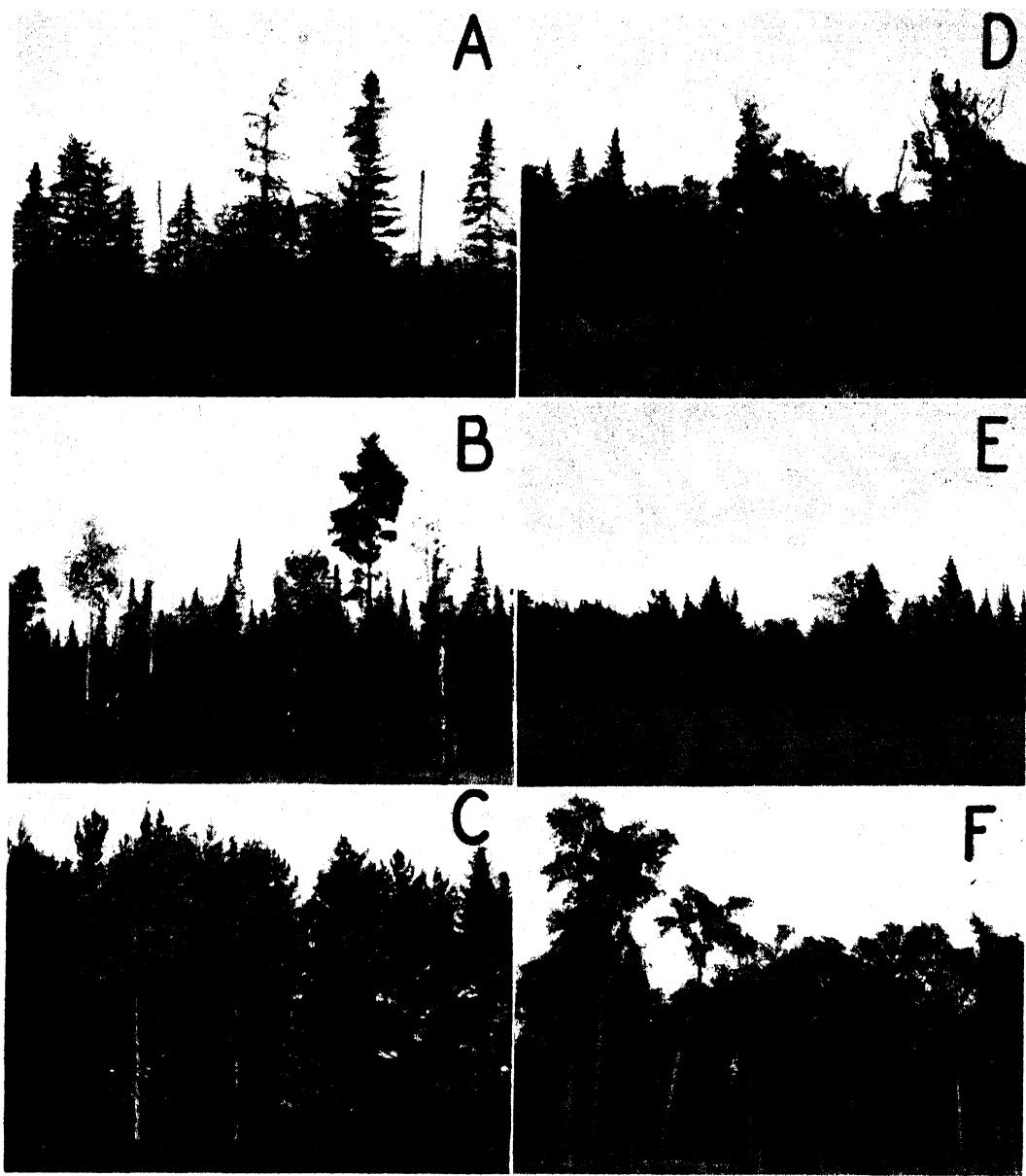
Fig. 5. Forest types in Podzol region of Wisconsin on soils influenced by ground water table (Oneida and Langlade Counties, Wisconsin). (*A*) Black spruce and tamarack on alpha-gley swamp-border sand; (*B*) mixed stand of white spruce, balsam fir, white pine, aspen and paper birch on beta-gley sandy podzol; (*C*) white and red pine with some aspen and white spruce on gamma-gley bor sand; (*D*) hard maple, red maple, rock elm and black ash with some balsam fir on alpha-gley podzol loam; (*E*) mixed stand of hard maple, basswood, American elm, white pine, balsam fir and white spruce on beta-gley podzolic loam; (*F*) hard maple and basswood on gamma-gley mull loam. *A*, *B* and *C*—Sandy outwash of recent glaciation; *D*, *E* and *F*—heavy drift of old glaciation.

TABLE I.   *Correlation of gley soils with the composition and growth of forest vegetation in Wisconsin*

| Soil | Stand | Yield at 100 yrs. cu. ft.* | Floristic site |
|------|-------|------------|----------------|
| *A.   Podzol Region.   Silty-clay loams derived from granitic drift of Pre-Wisconsin glaciation (Colby series, Langlade Co., Wis.)* | | | |
| Alpha-gley loam (Podzol) | Balsam fir, white spruce, some black ash and red maple. Understory of mountain ash, tag alder, willows, and dogwood. | 2,200 | *Sphagnum-Polytrichum-Carex-Equisetum* site |
| Beta-gley loam (Podzolic soil) | Hard maple, rock elm, red maple, some basswood, yellow birch balsam fir and white spruce. Hard maple and basswood inferior. Scattered dead balsams. | 3,500 | Fern site |
| Gamma-gley loam (Mull soil) | Hard maple, basswood, some white pine. Leatherwood and numerous other shrubs. Vigorous growth of sprouts. | 4,800 | *Adiantum-Thalictrum-Hydrophyllum* site |
| *B.   Degraded Prairie Soils Region.   Silt loams derived from recent calcareous drift (Miami series, Dane Co., Wis.)* | | | |
| Alpha-gley loam (Lowland prairie soil) | Lowland meadow. | — | *Carex* site |
| Beta-gley loam (Mottled grey forest soil) | Bur oak, black oak, some red oak, aspen and box elder. Abundant hazelnut in understory. | 1,900 | *Corylus* site |
| Gamma-gley loam (Nut-structured grey forest soil) | White oak, red oak, some black oak, walnut, hickory, white ash. | 3,200 | *Circaea-Amphicarpa-Psedera* site |

* Yields obtained by interpolation for fully stocked stands.
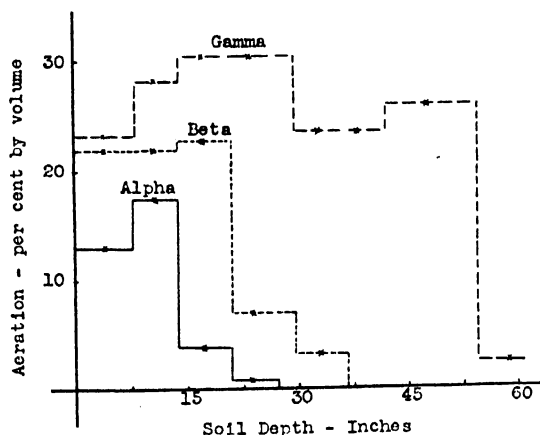


FIG. 6. Air contents of Alpha, Beta and Gamma gley soils determined as the difference between the porosity and field saturation.

Figure 6 contains the data of soil aeration determined by the Kopecký ('28) and Burger ('22) method as the difference between soil porosity and field saturation. The air content thus obtained appears to be the single physical factor best expressing the nature and growth conditions of gley soils.

The results of chemical analysis of gley soils from northern and southern Wisconsin are summarized in tables II and III. The gley horizons of the northern, podzolic soils are characterized by a slight decrease in acidity due to hydrolytic action of water, and partial destruction of the base exchange compound,

TABLE II.  *Analyses of gley podzol soils (Colby series) from vicinity of Bavaria and Summit Lake,
Langlade County, Wisconsin*

| Hori-zon | Depth of sampling | Reac-tion | Exch. capacity | Total N | Avail. P | Avail. $K_2O$ | Repl. Ca | Repl. Mg |
|---|---|---|---|---|---|---|---|---|
|  | Inches | $pH$ | $\frac{m.e.}{100}$ | Per cent | | P.p.m. | | m.e./100 g. |
| *Alpha-gley loam* | | | | | | | | |
| $A_0$ | 0–4 | 4.5 | 22.6 | 1.39 | 35.0 | 313.0 | 2.8 | 1.75 |
| $A_1$ | 5–7 | 4.3 | 35.2 | .28 | 41.5 | 85.6 | 2.8 | 1.86 |
| $A_2G$ | 10–14 | 4.3 | 3.2 | .07 | 43.0 | 86.6 | 1.6 | 1.43 |
| G | 15–18 | 4.8 | 3.0 | .03 | 22.0 | 50.3 | 1.6 | .77 |
| *Beta-gley loam* | | | | | | | | |
| $A_0$ | 0–2 | 4.8 | 61.5 | 1.68 | 66.5 | 948.0 | 24.3 | 6.46 |
| $A_1$ | 2–5 | 4.5 | 32.2 | 1.23 | 39.0 | 307.0 | 3.9 | 2.28 |
| $A_2$ | 10–14 | 4.3 | 6.0 | .06 | 15.0 | 27.8 | 2.7 | 1.10 |
| BG | 24–27 | 4.6 | 7.6 | .024 | 11.2 | 57.8 | 1.2 | 1.40 |
| *Gamma-gley loam* | | | | | | | | |
| $A_0$ | 0–2 | 6.5 | 61.6 | 1.05 | 224.5 | 1,290.0 | 54.7 | 19.50 |
| $A_1$ | 3–6 | 5.7 | 16.6 | .3 | 24.5 | 202.2 | 9.9 | 2.46 |
| $A_2$ | 9–12 | 5.0 | 4.2 | .01 | 29.5 | 39.6 | .6 | 1.46 |
| B | 24–27 | 4.5 | 6.6 | .016 | 24.0 | 80.3 | 2.3 | .99 |
| G | 54–58 | 5.0 | 6.6 | .012 | 21.0 | 71.4 | 2.6 | 1.14 |

apparently because of the reduction and solubility of iron. An accumulation of soluble phosphates in the gley layer is the outstanding feature of soils in the southern prairie-forest region. The general productivity level is higher in gamma gley soils than in the other varieties of these soils.

SUMMARY

The proposed classification recognizes three ecologically important types of hydromorphous soils, based on the depth of the ground water table or the upper limits of the gley horizon. *Alpha gley soils* (Shallow gley soils) or semi-swamp soils: gley layer protrudes through the A horizon at a depth of about 1 foot from the surface. *Beta gley soils* (Mid gley soils) or insufficiently drained, periodically wet soils: gley layer grades into B horizon, being 2 or 3 feet from the surface. *Gamma gley soils* (Deep gley soils) or sufficiently drained but adequately moist soils: gley layer occurs in C horizon, at a depth of from 4 to 7 feet.

Alpha gley soils support stands of water-loving species. Mosses and sedges form the characteristic ground cover. These soils are unsuitable to planting without artificial drainage. Deforestation or heavy cuttings may lead to further increase of moisture, invasion of mosses and development of swamp. These soils offer greater possibilities of drainage than peat deposits.

Beta gley soils are a transitional type suitable for the survival of both lowland and upland species, but not for their successful growth. Upland species suffer in the spring and fall from deficiency of aeration, whereas lowland species perish in the summer from drouth. The growth of stands is hindered by a deficiency of available nutrients, resulting from the shallow depth of root penetration. The

abundance of weakened specimens encourages the development of parasitic organisms and creates dangerous breeding centers. Artificial reforestation often requires the use of expensive mound or top-furrow planting methods. Sanitation is the chief objective of silvicultural cuttings. Because of the danger of windfall, shelterwood cuttings are preferable. Intercepting ditches or simple vertical tiles may be justifiable under special conditions.

A ground cover of mesophytic and hydrophytic plants and numerous fern species is indicative of this soil type. Nevertheless, beta gley soils are not readily discernible in nature, and the failure to recognize them often leads to serious silvicultural mistakes.

Gamma gley soils are characterized by the occurrence of more exacting species than are ordinarily found on upland soils of similar texture. Sufficient depth of

aerated soil, availability of nutrients, accessibility of ground water, and its relatively small seasonal fluctuation result in exceptionally rapid growth of stands and their general stability. In planting and logging it is necessary to consider the vigorous growth of competing vegetation, especially sprouts which greatly benefit from the deep ground water. Gamma gley soils may be formed artificially by skillful damming of streams. The nature of gamma gley soils can only be revealed by the use of a long extension auger or by investigation of deep profile pits. Forestry has suffered considerable losses because of the failure to realize the full potentiality of soils with available capillatum. Still greater losses were encountered because the successful growth of certain species on gamma gley soils encouraged the planting of the same species on texturally similar soils but with inaccessible ground water.

TABLE III.  *Analyses of degraded prairie gley soils (Miami series) from vicinity of Madison, Dane County, Wisconsin*

| Hori-zon | Depth of sampling | Reac-tion | Exch. capacity | Total N | Avail. P | Avail. K₂O | Repl. Ca | Repl. Mg |
|---|---|---|---|---|---|---|---|---|
| | *Inches* | *pH* | $\frac{m.e.}{100}$ | *Per cent* | | *P.p.m.* | | *m.e./100 g.* |
| | | | | *Alpha-gley loam* | | | | |
| A₁ | 4–7 | 6.9 | 50.2 | .355 | 39.0 | 71.3 | 34.7 | 12.7 |
| A₂G | 12–15 | 7.2 | 21.7 | .046 | 22.5 | 109.1 | 17.0 | 8.1 |
| G | 15–18 | 7.8 | 17.6 | .024 | 33.5 | 102.7 | 12.9 | 5.6 |
| | | | | *Beta-gley loam* | | | | |
| A₁ | 3–5 | 4.5 | 16.9 | .216 | 22.0 | 116.63 | 7.2 | 3.12 |
| A₂ | 10–12 | 5.5 | 8.4 | .024 | 18.0 | 109.14 | 4.4 | 2.49 |
| BG | 18–24 | 5.0 | 12.45 | .026 | 17.6 | 140.17 | 6.75 | 4.39 |
| G | 31–34 | 5.3 | 14.05 | .026 | 48.0 | 123.25 | 7.25 | 5.09 |
| | | | | *Gamma-gley loam* | | | | |
| A₁ | 0–4 | 6.3 | 20.4 | .286 | 27.5 | 237.5 | 15.9 | 3.7 |
| A₂ | 8–12 | 5.6 | 6.4 | .050 | 24.5 | 145.5 | 3.8 | 1.7 |
| B₁ | 20–24 | 5.3 | 14.1 | .034 | 25.0 | 177.6 | 5.6 | 3.7 |
| B₁ | 32–36 | 5.0 | 18.1 | .034 | 31.0 | 119.8 | 8.2 | 5.3 |
| B₂ | 48–52 | 5.8 | 9.5 | .024 | 31.0 | 115.6 | 5.5 | 4.3 |
| B₂G | 56–60 | 5.4 | 11.7 | .024 | 54.5 | 94.2 | 6.4 | 2.8 |

The workability of the proposed classification is illustrated by two concrete examples presenting the correlation between gley soils and forest growth in podzol and prairie-forest regions of Wisconsin.

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# SOME OBSERVATIONS ON THE PHYSIOLOGY OF
## WARM SPRING FISHES [1]

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Numerous experiments upon cold-blooded animals have shown that their respiratory metabolism is a function of the temperature to which they are subjected. In the case of fishes, several criteria of respiratory metabolism have been employed: (1) actual oxygen consumption, as revealed by direct measurement; (2) oxygen requirement, as indicated by (a) survival time in deoxygenated water, or (b) survival time in dilute potassium cyanide solution. In this laboratory, all three of these procedures have been employed, with results which appear to be in substantial agreement (Sumner and Doudoroff, '38). At different temperatures, the reciprocals of the times of survival of fishes in thousandth-molar KCN solution are in very nearly the same ratio as the measured rates of oxygen consumption at the same temperatures, while the ratio for survival time in boiled sea-water may be regarded as reasonably close.

The mean $Q_{10}$ for respiratory metabolism in *Fundulus parvipinnis,* based upon direct measurements of oxygen consumption by Wells (1935, table II, experiments 4 and 5, means of three figures: 10° to 20°, 12° to 22°, and 14° to 24°) was 2.90. The mean $Q_{10}$ for the goby, *Gillichthys mirabilis,* within approximately the same temperature range, based upon reciprocals of survival time in KCN solution, was 2.84 (Sumner and Doudoroff, '38, table I). The corresponding figure, based upon a much smaller series, tested in boiled sea-water, was considerably lower, it is true, *viz.,* 2.49.

Further experiments have shown that the initial change in susceptibility to cyanide, resulting from an increase or decrease in temperature, was followed by a "recoil," such that the departure of each lot from its original metabolic level diminished somewhat with the lapse of time. Graphs (Sumner and Doudoroff, '38, fig. 2) show that the greatest difference between two lots kept at contrasting temperatures is manifested shortly after their first being subjected to these temperatures. Thereafter the difference diminishes for a few days. This process of physiological adaptation appears to be brief, however. After ten days or less, there is no further visible convergence of the curves for the two lots, kept at 10° and 30°, respectively. These continue to manifest the greater part of the original difference, their mean periods of resistance to KCN, at the end of a month, standing in the ratio of about 6 to 1.

So far as we know, previous tests of the relation of temperature to the respiratory metabolism of fishes have concerned themselves with changes under laboratory conditions, the duration of the treatment being at most a few months. That fishes living under natural conditions in warm and cold waters should maintain throughout their lives such extreme differences in oxygen consumption would seem on first thought unlikely. This if only because we know that some of the most active fishes (*e.g.* the trouts of mountain streams) spend their lives in cold waters.

It has long seemed desirable that comparative tests of metabolism should be made upon fishes in nature, preferably in some case in which isolated populations of the same or closely related species are found in waters of widely different temperature. It is well known that members of the genus *Cyprinodon* occur in numer-

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ous desert springs in California and neighboring parts of Nevada. Much less generally known is the existence of another genus of poeciliid fishes (*Crenichthys* Hubbs) which appears to be rather widely distributed in the springs of eastern Nevada. Many of these springs are warm or temperate ones, which are believed to maintain fairly constant temperatures throughout the year. In some cases, at least, these fishes appear to restrict themselves very largely to the actual sources of flow, not venturing far into the brooks or creeks which proceed from them. So far as this is true, their thermal environment must present little variation throughout their lives. This group might be expected to furnish, therefore, particularly favorable material for experimental studies of the type above suggested.

In April and May, 1939, the authors spent two weeks in the field, in quest of *Cyprinodon* and in experiments upon one species of this genus. Later in the year (October), another two weeks were devoted to field studies of *Crenichthys*. Our advance information regarding the occurrence of both of these fishes was received almost wholly from Mr. R. R. Miller, of the University of California (now of the University of Michigan), who provided us with abundant records of field data, obtained by Professor C. L. Hubbs and himself. Our thanks are due Mr. Miller for indispensable help in this connection.

Members of *Cyprinodon* inhabiting these various desert springs have been generally referred to a single species, *C. macularius* Baird and Girard. Pronounced local differences in size and color are evident among these fishes, however, and recent students believe that some of these forms deserve specific rank. Likewise, but a single species of *Crenichthys* (*C. nevadae* Hubbs) has thus far been described (Hubbs, '32), though it is possible that the occurrence of these fishes in isolated springs has led to their subspecific or even specific differentia-

tion.[2] However, these taxonomic questions hardly seem relevant to our present discussion and we have attempted no taxonomic study of the specimens collected by us. We understand that such studies are being conducted by others.

Both of the species here under consideration are small fishes, rarely reaching a length of 6 centimeters. *Crenichthys* differs from *Cyprinodon* in altogether lacking the pelvic fins and in dental and some other characters. There are considerable sexual differences in color and markings, and, particularly in *Crenichthys*, there is wide individual variability in these respects.

*Fish Slough, California.*—As our intended "cold" station, we first visited Fish Slough, some ten miles north of Bishop, California, where *Cyprinodon* was known to occur, and where the water was believed to remain low (20° C. or below) throughout the year. Fish Slough (U. S. G. S., "Bishop" Quadrangle) is essentially a creek, bordered by narrow strips of marshy land, and heading in a considerable number of large springs.

It had been planned to transport fishes from these springs to the warm-spring region next to be visited in Nevada. Although this proved to be impossible, a brief statement regarding these fishes and their habitat seems worthwhile.

While never concentrated in schools of any size, they were present in some numbers in or near the springs. Nearly a hundred were caught by our party with seine and dip-net, within the course of a few days, and without greatly depleting the visible stock. Of the specimens captured, the sex of only 60 was recorded. Twenty-five of these were males, 35 females. The water temperature, on April 23–27, in and near the springs, ranged

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[2] Since writing the foregoing, we have learned from Dr. Hubbs (personal communication) that he now recognizes a second species of *Crenichthys* (*C. baileyi* Hubbs), and that the specimens obtained by us are to be referred to this species.

from 19.2° to 20.8° C.[3] The fishes appeared to be in full sexual activity. Spawning movements were continually observed, though it was impossible to approach closely enough to witness the actual discharge of eggs.

We were surprised by the low viability of these fishes in captivity, since "desert minnows" of this genus have frequently been transported successfully to aquaria in San Francisco and elsewhere (Cf. also experiments with *Crenichthys*, below). Our specimens frequently died within a few hours after capture, although handled with great care, and the majority of them died within a day or two, even when kept in screen cages immersed in the springs from which they had been caught. Very few reached our Nevada camp alive, and these were presumably in no condition for physiological tests. There was no appearance at any time of asphyxiation. This unexpected mortality may possibly have been due to exhaustion from prolonged sexual activity, which seemed to continue unabated in the cans or cages in which the fishes were forced into rather close association.

*Ash Meadows, Nevada.*—For the foregoing reason, our tests of metabolism on this trip were restricted to the "Ash Meadows" district of the Amargosa Desert, in southwestern Nevada, about 12 miles from Death Valley Junction, California. This region abounds in springs of considerable size, having temperatures ranging from 23° to 33.5° C. Most of these springs, together with their outflowing streams in the immediate neighborhood, are inhabited by *Cyprinodon*, sometimes in great abundance. Some of them contain other small fishes (Cyprinidae).

The highest temperature noted (33.5°) was in Devil's Hole, a shallow cave containing a small pool, the outlet from which does not flow above ground. Here occurs a minute, dark colored *Cyprinodon*, which

has been provisionally described by Wales ('30) as a distinct species (*C. diabolis*). The entire existing population of this form can hardly exceed a few hundred individuals.

Our experiments were restricted to the two springs in this locality which displayed (nearly) the greatest contrast in temperature, and from which *Cyprinodon* could be obtained. The warm spring was on the ranch of Ora Lovell, the cool one on the ranch of R. M. Tubb. We are indebted to Mr. Lovell and to Mr. Tubb and his family for the opportunity to catch our specimens and for other favors.[4]

These experiments, though decisive on some points, were rather rigidly restricted by the time at our disposal and by the extent of one of the two essential populations. It was even necessary to omit at this time the obviously important experiment of testing the cool spring fishes at the temperature of the warm spring.

The Lovell spring, at the time of our visit (April 28 to May 1) had a temperature of 32.5° to 33° C. This temperature did not fall appreciably between the points of outflow and the nearby pool, where the fishes congregated in large numbers, and from which most of our specimens were caught with a small seine.

The temperature of the Tubb spring maintained itself (April 28 to May 4) at 23.8° to 24°.[5] The supply of *Cyprinodon* was much more limited here. Most of our specimens were caught, one at a time, with a dip-net.

The successful experiments involved the determination of the survival time of these fishes in 0.001 M KCN. Death, in these experiments, was counted from the

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[3] Mr. Miller reports a temperature of 64° F. (17.8° C.) for August 2, 1937. This is rather surprising, considering that our readings were made in April.

[5] The temperatures recorded by us for both of these springs agree almost precisely with those found by Dr. Hubbs and Mr. Miller during a previous summer.

moment that an individual ceased to make any visible movements, either spontaneous, or provoked by poking with a glass rod. The conspicuous death-throes, described for *Gillichthys* (Sumner and Doudoroff, '38), were rarely shown by *Cyprinodon*. Our experiments were of three sorts:

(1) Fifty-two specimens (33♂, 19♀) from Lovell's spring (warm) were tested at approximately their habitual temperature. They were placed, about 30 minutes after capture, in KCN solution, in three bowls, immersed in the water from the spring. The temperature in the bowls commenced with 32.5°, falling to 31.5° toward the end.

(2) Thirty-three fishes (21♂, 10♀, 2?) caught in Tubb's spring (cool), were tested at the approximate temperature of the latter. The temperature in the bowls was 23.8° ±, falling 1° or less during the tests. Three tests were made on different days.

(3) Forty fishes from Lovell's spring (20♂, 20♀) were brought almost immediately to Tubb's, their water temperature being allowed to fall to that of the latter. About one hour after capture they were placed in KCN in three bowls, immersed in the stream from the spring. The temperature in the bowl was 23.7°, falling only 0.2° at the end.

The mean survival times of these three series are given in table I.

TABLE I. *Mean survival times of fish in KCN solution*

| | Number of fishes | Time in minutes |
|---|---|---|
| Lovell's at Lovell's | 52 | 41.6 |
| Tubb's at Tubb's | 33 | 65.0 [6] |
| Lovell's at Tubb's | 40 | 96.0 |

The possibility that the differences among these three series resulted from any

[6] The times recorded for the three separate tests here averaged were: (1) 91.3 (6 fishes); (2) 53.8 (16 fishes); (3) 66.8 (11 fishes). The high first figure is largely due to the prolonged survival of a single individual (see figure 1 (2)).

chance differences in the proportions of males and females seems to be excluded. The array of values in the largest series (series 1, fig. 1), reveals no tendency toward a bimodal distribution. It must likewise be pointed out that the sex-ratios of series 1 and 2 were not widely different from one another, although series 3, it is true, differs greatly from the other two in this respect. The excess of males recorded for the Ash Meadows fishes as a whole contrasts with the situation at Fish Slough, where females rather heavily preponderated among the specimens saved. That the former circumstance was not altogether due to a tendency on our part to select larger individuals for experiment (the males are larger than the females), is shown by the composition of the Tubb's spring lot, which includes nearly all the individuals taken. Since a preponderance of males is quite unusual in a fish population, it is possible that the males frequented more accessible parts of this very deep spring.

It was not regarded as necessary to measure these fishes, as had been done in the goby experiments, since it was determined for the latter that size, within very broad limits, played no part in susceptibility to cyanide. Casual observation pointed to a similar lack of correlation in the case of *Cyprinodon*.

Histograms (fig. 1) show the mortality rates of these three sets of fishes. The probability that the difference between the mean value of series 1 and that of either series 2 or 3 is accidental is much less than 1 in 10,000. In the case of the difference between series 2 and 3, the probability is considerably greater, though still small, viz.: about 35 in 10,000.

Of course, statistical probabilities such as these serve merely to exclude "chance" (*i.e.*, random sampling) as an explanation of the differences in question. The actual cause of the differences may be quite irrelevant to the objects of the experiment. In this connection, it is important to state that our later series of experiments with another species of fish
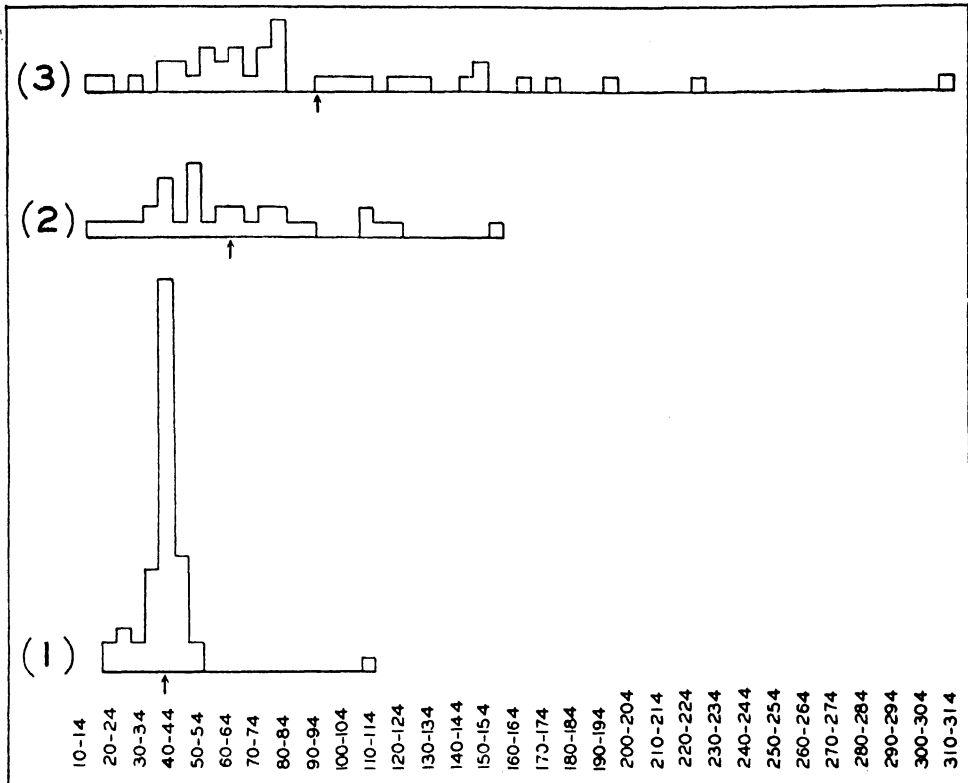
FIG. 1. Time of survival of *Cyprinodon* in thousandth-molar potassium cyanide. (1) Warm-spring fishes, tested at their normal temperature (32.5°). (2) Cool-spring fishes, tested at their normal temperature (23.8°). (3) Warm-spring fishes, tested at temperature of cool-spring. Abscissas denote times in minutes. Each square represents an individual fish. Arrows indicate means.

(p. 52) failed to indicate any such superior resistance on the part of warm-spring individuals, when transferred to a cool spring, in comparison with those native to the latter. This difference between our two sets of results may, however, depend upon differences in the species employed, or upon differences in their environmental conditions, so that we seem warranted in admitting the possibility that the picture presented by our table I and figure 1 represents the typical reactions of *Cyprinodon* (sp?) under the three stated sets of conditions.

It will be noted that the mean survival time of the warm-spring fishes at the cold-spring temperature (96 minutes) was 2.31 times that of these same fishes at their own habitual temperature (41.6 minutes). Since the difference in tem-

perature between these two springs was close to 9° C. the $Q_{10}$ for respiratory metabolism, as thus revealed, was 2.5 ($= 2.31^{10/9}$).

No very exact comparison with $Q_{10}$ figures for the goby *Gillichthys* (Sumner and Doudoroff, '38) is possible, owing to differences in the conditions of the two sets of experiments. Not only were the temperature ranges different in the two cases, but most of the figures for *Gillichthys* are based upon experiments in which the tests were made from one to many days after the transfer of the fishes to warmer or cooler water. Such tests were impossible in the case of *Cyprinodon*, owing to the difficulty of maintaining this fish in health for so long a period.

For gobies, the $Q_{10}$ figure, between 20° and 30°, based on fishes which had been

kept for some weeks at the latter temperature, was 2.1; while the figure based on fishes kept for a very brief period (from a half hour to five hours) at this temperature was 2.0 (Sumner and Doudoroff, '38, table II). The latter figure is probably more fairly to be compared with the figure above stated for *Cyprinodon*, although the temperature change was in the opposite direction.

If, on the other hand, we compare the metabolic rate of the Tubb spring (cool water) fishes at their accustomed temperature (series 2) with that of the Lovell spring fishes at their accustomed temperature (series 1), we find an increase, per 9° of 1.56, indicating a $Q_{10}$ of 1.6. One might be tempted to hold that the difference between this figure and the one which is based upon a comparison of series 1 and 3 (2.5) furnished a rough measure of the degree of divergent temperature acclimatization which our two populations had undergone. However, the failure of *Crenichthys* to manifest similar relations weakens the case for this interpretation of the phenomena.

In view of the foregoing considerations, it was regarded as important, after our visit to eastern Nevada in the fall, to repeat, in part, our Ash Meadows experiments. A serious attempt was made to do this, but changes which had been made in the outflow of the water at the Tubb spring rendered this impossible.

*White River Valley, Nevada.*—Despite its name this valley contains no continuous, permanent river, at least at the levels visited by us. It contains, however, numerous large springs having various temperatures. Our headquarters for about two weeks in October, 1939, were made near Preston, White Pine County, close to a large spring, or group of springs, having relatively low temperatures. "Preston Spring," as we shall designate this, is the source of a creek of considerable size, which is used locally for irrigation purposes. Its temperature, at several of the points of outflow, was 21.0° C., throughout the period of our visit (October 4 to 16).[7]

Small fishes of several species are abundant in the upper reaches of this creek. Besides *Crenichthys baileyi* Hubbs, a catostomid (*Pantosteus* sp.) and a cyprinid (*Rhinichthys osculus*) were taken. These were all kindly identified for us by Dr. Hubbs. The first named, which was our main object of interest, could be caught in dip-nets in sufficient numbers for experimental purpose. Another favorable circumstance was the ability of these fishes, both those from the cool and the warm spring, to withstand captivity and transportation with little or no resulting mortality.

The warm spring with which we were concerned is known locally as "Mormon Spring." It is located in Nye County, about thirty miles to the south of Preston and about 6 miles west of Riordan's

[7] This is slightly lower than the figure (71° F.) given by Dr. Hubbs for August 26, 1938.

TABLE II.  *Oxygen determinations from two Nevada springs*

| Preston Spring (cool) | | | Mormon Spring (warm) | | |
|---|---|---|---|---|---|
| Locality | Number of samples | ml O₂/l | Locality | Number of samples | ml O₂/l |
| Source 1 | 4 | 2.04 | Source | 2 | 0.38 |
| Source 2 | 2 | 2.25 | West ditch, below small | | |
| Source 3 | 2 | 2.14 | spillway | 2 | 2.09 |
| Creek, ¼ mile below sources, | | | Same, farther down | 2 | 2.56 |
| sunrise | 1 | 2.94 | East ditch | 2 | 2.12 |
| Same, 3 P.M. | 2 | 4.35 | | | |

ranch. The temperature of this spring, at its main point of outflow, is almost exactly 37.0° C. *Crenichthys* was abundant here, but no other fishes were seen. While they swam freely into the warmest water, most of our specimens were obtained some yards further down-stream, where the temperature fell to 36° or even lower.

Oxygen determinations by the Winkler method (table II) showed that the waters from these two springs differed widely in respect to oxygen content at their sources. That discharged by the warm spring contained about a sixth as much oxygen as that from the cool one. It will be seen, however, that the former water soon acquires an oxygen content closely similar to that of the latter, after exposure to aeration and to the photosynthesis of algae. The effects of these influences upon the water of Preston Spring are likewise shown.

Tests of metabolic rate, by the cyanide method, were made in four series of experiments. (table III). In each of these experiments, it was our practice to immerse the bowls containing the KCN solution in the water of the spring where the test was made, with the object of keeping them at the temperature of the latter. In reality, however, the temperature in the bowls commonly fell from 1.5° to 3° C. in the course of the experiments. In experiments involving transfer from one spring to the other, the fishes were carried in somewhat insulated 3-gallon bottles. This involved a delay of several hours, during which the water temperature fell about five degrees.

TABLE III. *Mean survival times of warm-spring and cool-spring fish in KCN solution in water of their own and another spring*

|  | Number of experiments | Number of fishes | Mean survival times | Coefficient of variation |
|---|---|---|---|---|
| (1) Mormon at Mormon | 3 | 48 | 9.67 | 14.9 |
| (2) Preston at Preston | 3 | 83 | 44.7 | 15.9 |
| (3) Mormon at Preston | 3 | 98 | 41.9 | 18.0 |
| (4) Preston at Mormon | 5 | 52 | 5.81 | 16.5 |

Table III gives the mean survival times and other data for these various tests, while figure 2 presents the distribution of frequencies.[8]

(1) The mean survival time of the first series (warm-spring fishes tested at their customary temperature) is about 0.22 that of the second series (cool-spring fishes tested at their customary temperature), if the figure for the latter which appears in the table be employed. It is 0.24, if a rejected experiment (see next paragraph) be included. Another comparison of interest is that between the survival time of the warm-spring fishes when tested in the latter, and that of the cold-spring fishes when transferred to the warm spring. It will be seen that the former is 66 per cent greater than the latter. This point will be discussed below.

(2) The "Preston at Preston" series, as included in table III, comprises three experiments, the mean survival times for these being 40.5, 43.5 and 51.9 minutes, respectively. In each case, the fishes were kept over night in screen cages, immersed in the spring, before the test was made. A fourth experiment, based upon 44 individuals, has been rejected from this series, owing to the somewhat enfeebled condition of the fishes.[9] The mean survival time of this lot was 29.7 minutes. To include these would lower the grand average to 39.5.

The figures for these first two series —9.67 and 44.7 (or 39.5) minutes—afford a comparison of the resistance to KCN of two lots of fishes dwelling in environments differing by about 15° C. in temperature. They indicate a $Q_{10}$ of 2.8, or 2.6, if the more inclusive of the foregoing means is accepted for the Preston fishes. These figures approximate certain of those for the $Q_{10}$ as determined

[8] Identification of the sexes was impossible in so many cases that we have thought it best not to give any figures for these. Apparently the females were greatly in excess.

[9] This lot was exceptional in having been subject to a considerable mortality during the preceding 24 hours.

the $Q_{10}$ figure observed in transferring Lovell's spring fishes to Tubb's spring, though not that based upon Lovell's and Tubb's spring fishes at their own natural temperatures, which is considerably lower (Cf. p. 50).

(3) The "Mormon at Preston" figures are likewise based upon several experiments. In this case, the conditions were purposely made somewhat different in the different experiments. In one case (a), the test was made without any preliminary sojourn in Preston Spring water. In the second case (b) the fishes were kept in a screen cage, in the Preston Spring for 2½ hours before the test. In the third case (c), they were kept in the latter for 14 to 15 hours before the test. The means for these separate experiments are 43.4, 43.3, and 37.0 minutes, based upon 34, 42 and 22 fishes, respectively. The lower value for the last lot is of highly probable significance, statistically speaking (only 2 chances in 10,000 that it is "accidental"), though it is not, of course, certain that this difference is due to their longer sojourn in the cool water (Cf. differences among the "Preston at Preston" lots, where no such explanation can be employed).

Somewhat disconcerting is the fact that the "Mormon at Preston" series as a whole showed a slightly *lower* mean resistance than the fishes which were native to the Preston Spring. This difference is of the opposite sign to that found by us in the comparable experiment in Ash Meadows (fig. 1). Moreover the difference is of rather probable significance (3.7 × P. E.). It is possible that transfer to water 15° C. lower (the difference at Ash Meadows was only 9°) resulted in a lessened resistance to cyanide, in the case of the Mormon Spring fishes, which outweighed the favorable effects of the lowered metabolic rate.

On the other hand, it seems possible that these differences between our results with *Cyprinodon* and with *Crenichthys* represent actual physiological differences between these two genera. In this re-



FIG. 2. Time of survival of *Crenichthys:* (1) Warm-spring fishes tested at (nearly) their normal temperature (35.5°–36°). (2) Cool-spring fishes, tested at (nearly) their normal temperature (21°). (3) Warm-spring fishes tested at temperature of cool spring. Shaded areas represent fishes kept over night in latter. (4) Cool-spring fishes tested at temperature of warm spring (see fig. 1).

from laboratory studies of the goby *Gillichthys,* though not very closely that figure which is most nearly comparable with them. They likewise approximate

spect, comparison is interesting between our experiments and some recently reported for certain invertebrates (Fox, '36; Fox and Wingfield, '37).

(4) The low survival time of the "Preston at Mormon" series in comparison with all the others, including the "Mormon at Mormon" series, has already been pointed out. The superior resistance of the latter might be expected on the supposition that the resident fishes had, as a result of physiological adaptation, a lower metabolic rate than those which had been recently introduced from a lower temperature (Cf. Sumner and Doudoroff, '38). However, it would also be possible to interpret this lower viability of the introduced fishes as due to the cumulative effect of two lethal agencies, heat and cyanide. There is no doubt that even moderately high temperatures have a lethal effect upon fishes quite independent of their effect upon oxygen consumption.

In addition to the foregoing experiments, involving determinations of survival time in KCN, several tests were made of the more direct effects of transferring these fishes from cool to warm water and vice-versa.

(1) About 60 specimens of *Crenichthys* were taken from Preston Spring to Mormon Spring in two of the large bottles already referred to. The temperature of their water was raised in about ten minutes from 20.5° to that of the ditch in which they were placed in two screen cages (35.2°). On the following day, all of these fishes were dead, with the appearance of having been so for some hours.

(2) Twenty-four Preston Spring fishes were taken by bottle to Mormon Spring. The water in the bottle was immersed and warmed throughout a period of an hour to nearly the temperature of the spring. The fishes were then transferred to a screen cage in the outflow from the spring, at a point where the temperature was 36° and the oxygen content 2.09 ml. per liter. The majority of the lot were soon unable

to right themselves in the water current and drifted helplessly against the sides of the cage. Within less than half an hour, one or two appeared to be dead; while in 1¾ hours all were dead.

(3) In contrast with the foregoing, 14 Mormon Spring fishes which had been kept in Preston Spring for 43 hours, and which had shown no unhealthy symptoms during that time, were brought to Mormon Spring and placed in another cage, alongside those discussed in the preceding paragraph. All of these were living and apparently well on the following day, after 24 hours at the higher temperature, with the exception of a single individual which had probably died early in the experiment. Thus a sojourn in the cool spring for nearly two days had not appreciably affected the adaptation of these fishes to the high temperature.

The death of the cold-spring individuals in warm water seems to have been due neither to the greatly reduced oxygen content of the latter nor to the heightened oxygen requirements of the fishes themselves. This is rendered probable by two circumstances: (1) the oxygen content, at the points where the experiments were actually performed, was nearly or quite as great in Mormon Spring as in Preston Spring; (2) fishes of the warm-spring population swim freely into the immediate vicinity of the point of outflow, and thus into water having an oxygen content not more than a sixth that of the stream a short distance below. Many fishes are known to be able to adjust themselves to widely different oxygen concentrations in their medium.

## Summary

(1) Fishes (*Cyprinodon* sp.) inhabiting a warm spring, at 32.5°–33° C. were found to have, at this temperature, a mean survival time, in thousandth-molar potassium cyanide, only 64 per cent of that shown by individuals inhabiting a cooler spring (23.8°–24.0°) at the latter temperature. From this it is perhaps fair to infer that under natural conditions, the

respiratory metabolism of the fishes inhabiting this warm spring is more than one and a half times as high as that of those inhabiting the cooler spring.

(2) Fishes of another poeciliid genus (*Crenichthys*) inhabiting a considerably warmer spring (35.5° to 37.0°) were found to have a survival time less than a fourth (0.22) of that shown by individuals inhabiting a cool spring (21.0°), when each series was tested at its own habitual temperature. This seems to indicate for the former a metabolic rate four or more times that of the latter.[10]

Although in each of these cases, it is likely that the two contrasted populations have been separated for a long period, probably some thousands of years, and that the temperatures of their habitats have differed rather widely throughout this period, we must conclude that such physiological adaptation as may have occurred has not been sufficient to bring about any considerable approximation of these metabolic rates.

(3) Whether or not any physiological adaptation in respect to metabolic rate occurred, such that individuals of two contrasted populations would show measurably different survival times if tested under the same temperature conditions, is not altogether certain. *Cyprinodon* seemed to furnish some evidence for the existence of such a modification, when samples of the two populations were subjected to the cyanide test at the lower temperature. The converse experiment (testing the two populations at the higher temperature) was not performed with this fish. *Crenichthys*, on the contrary, failed to reveal any probable difference corresponding to that shown by *Cyprinodon*—indeed there was a slight difference in the opposite direction—when tested in the cooler water. The converse experiment, however, revealed a marked difference in resistance to KCN between the

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[10] Referring, of course, to the actual, not the potential metabolic rate, *i.e.*, to that maintained under the normal life conditons of each population.

two respective lots, the cool-spring fishes, in warm water, succumbing considerably more rapidly than those native to the latter. As we have stated, however, this result is subject to another possible interpretation, not involving any assumptions respecting the relative metabolic rates of the two lots of fishes.

(4) Quite apart from any such problematic effects, in the direction of adaptation, upon the metabolic rate of these fishes, we have observed certain undoubted physiological differences between the warm-spring and cold-spring individuals. It was shown for *Crenichthys* that warm-spring specimens could be transferred to the cold-spring for two days (time did not permit of a longer test) and returned to the warm spring, without apparent harm, whereas specimens native to the cold spring were speedily killed by transfer to the higher temperature. Reasons were given for believing that the death of the cold-water fishes in warm water was due to other factors than the reduced oxygen content of the latter or the heightened oxygen requirements of the fishes themselves.

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# PLANT SUCCESSION DUE TO OVERGRAZING IN THE *AGROPYRON* BUNCHGRASS PRAIRIE OF SOUTHEASTERN WASHINGTON

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## INTRODUCTION

During the period when southeastern Washington was settled by white man the bunchgrass prairies, which covered large areas in this region, were used chiefly for grazing cattle. This industry had scarcely become established when it was demonstrated that the deep loessal soils characteristic of the region were excellent for growing wheat. Starting about 1880 this new type of land use began to replace the earlier, and by about 1910 all areas except those on which cultivation was either impractical or impossible had been brought into cropland. The remaining areas, the so-called "scablands," where the soil is shallow, or stony, or the surface is too frequently interrupted by such outcrops, have remained as grazing lands and probably will be used in this manner in the future. Within the last few decades the livestock industry in this region has undergone a second great change due to the replacement of the cattle by sheep over most of the range lands.

Wherever the soil of the non-agricultural land was deeper than about 1.5 dm. and was not sandy, the original bunchgrass cover was apparently identical with that of the deeper soils. As a result of long continued heavy grazing of these grasslands, the appearance and the forage value of the primeval prairie have been considerably changed. The bunchgrass, a climatic climax, has undergone a retrogression which in many cases has culminated in a biotic climax. The latter is as permanent as the present system of spring-fall sheep grazing.

An excellent opportunity of studying this vegetational retrogression exists today in northeastern Franklin County and adjacent Whitman County. Here, in different areas, exist fragments of the climatic climax in essentially virgin condition, several stages of retrogression, and in some cases the end point in this biotic succession appears to have been attained.

## CLIMATE

Precipitation records within the area of study consist of observations from 1899 to 1903 at Hooper, Washington (U. S. D. A. Wea. Bur., '36). During this period the mean annual precipitation was 31.2 cm., which includes a snowfall averaging 26.7 cm. each year. Calculations based on considerably longer records at Lacrosse and Lind, which are just outside the area studied, indicate that the average precipitation at Hooper is approximately 29 cm.

Considerably over half the annual precipitation occurs during the winter. Almost exactly half of the annual sum falls during the four months of November, December, January, and February.

At Lacrosse the average maximum temperature of the hottest month (July) is 31.5° C. with the average minimum of the coldest month (February) — 6° C. The average annual extremes of temperature are 43° C. and — 33° C.

Some evaporation figures for the summer months are available (U. S. D. A. Wea. Bur., '36) for Lind, Washington, which is situated about 43 kilometers northwest of the center of the area of study. These data make possible the calculation of the precipitation/evaporation ratios for the summer months at that station (table I), and such ratios are probably very similar to those in the region where the successional studies were made.

The growing season ends in early summer at which time the soil moisture becomes practically exhausted. During the dry mid-summer and early fall the sheep

TABLE I. *Some average precipitation and evaporation data at Lind, Washington: 1926 through 1930 (U.S.D.A. Wea. Bur., '36)*

| Month | Evapora-tion in cm. | Precipita-tion in cm. | Prec./Evap. ratio |
|---|---|---|---|
| April | 13.60 | 0.81 | .059 |
| May | 19.14 | 1.27 | .066 |
| June | 21.74 | 2.03 | .093 |
| July | 27.75 | 1.02 | .037 |
| August | 22.97 | 1.17 | .051 |
| September | 13.85 | 2.46 | .178 |

are taken to the mountains for grazing. In late fall when the rainy season returns, the perennial grasses and forbs and a few annuals such as *Bromus tectorum* put out new leaves and again afford green forage until the colder part of winter. In mid-winter, when no other forage is available, the dead shoots of *Agropyron* are grazed, at which time they may be eaten to the ground line.

## METHODS

Most studies of plant succession, including the present one, are made by analysing a group of associations which are then arranged in a sequence illustrating the investigator's concept of the stages through which the final stage has gone. Such a procedure is necessary chiefly because of the great expanse of time which would be required to observe the succession from beginning to end on the same plot. This method opens a way for fallacious conclusions, since one of the most fundamental principles of the scientific method can be so easily violated. Obviously, a study of the effects of variation of a single factor become significant only when all other factors remain constant. In any study of the grazing factor, one must have evidence that the original vegetation was essentially identical at all the stations which are analysed, and that the environment, except for the herbivores, was uniform.

All stations occurred within an area having a diameter of 32 kilometers and the elevation varied from 292 to 445 meters above sea level. These features

insure a relatively uniform climate at all stations.

In every case the topography is quite level.

To demonstrate that the soils at each of the four study areas are well within the range of texture (which is one of the most important aspects of soils in this region) and depth which allow a good development of the bunchgrass association, a comparable series of wilting coefficient determinations was made at each station. The water-holding power of the soil as indicated by the wilting coefficients in table II, is in all cases well within the

TABLE II. *Wilting coefficients of soils as determined indirectly from the hygroscopic coefficients (W.C. = H.C./0.68)*

| Decimeter horizons | Station 1 | Station 2 | Station 3 | Station 4 |
|---|---|---|---|---|
| 1st | 7.9% | 8.4 | 7.9 | 8.2 |
| 2nd | 9.5 | 8.9 | 8.9 | 9.0 |
| 3rd | 8.1 | 10.3 | 9.2 | 8.5 |
| 4th | 8.0 | 9.2 | 9.0 | 7.6 |
| 5th | 7.0 | 9.7 | 8.3 | 8.5 |
| 6th | 6.6 | — | 8.9 | 8.7 |

range which is favorable to this community in our region. Other observations by the writer have shown that this association is apparently normally developed in this region on soils as shallow as 1.5 dm., a soil depth which is well exceeded on all the areas studied.

A check on the uniformity of the original cover is the presence of all of the dominant or characteristic plants in the immediate vicinity of all stations. Careful attention to this point indicated that the original vegetation was at least floristically comparable in all cases.

The area of bunchgrass which approximates the virgin ungrazed condition is on a spur projecting into the Palouse River Canyon. When the railroad was built parallel to the canyon, the end of this spur was severed from the remainder of the prairie by a steep-walled cut about 10 m. deep, and thus has remained absolutely free from grazing for twenty-seven years.

Other areas apparently in near-virgin condition are very similar to this stand, hence the assumption of its undisturbed nature seems to be well supported.

The abundance and stature of the *Agropyron* plants was taken to be an indicator of the relative severity of grazing. Actual records of the kinds and numbers of animals and the periods of range use would be difficult if not impossible to ascertain and to evaluate in the

areas studied. The decrease of palatable plants and increase of non-palatable ones both point to the validity of my assumptions of the proper sequential arrangement of the stations.

A statistical comparison of these grazed and ungrazed areas of grassland was made by the frequency method. In each of four areas considered (figs. 1, 2, 3, and 4), a station consisting of 100 frequency plots was studied. The plots were $2 \times 5$
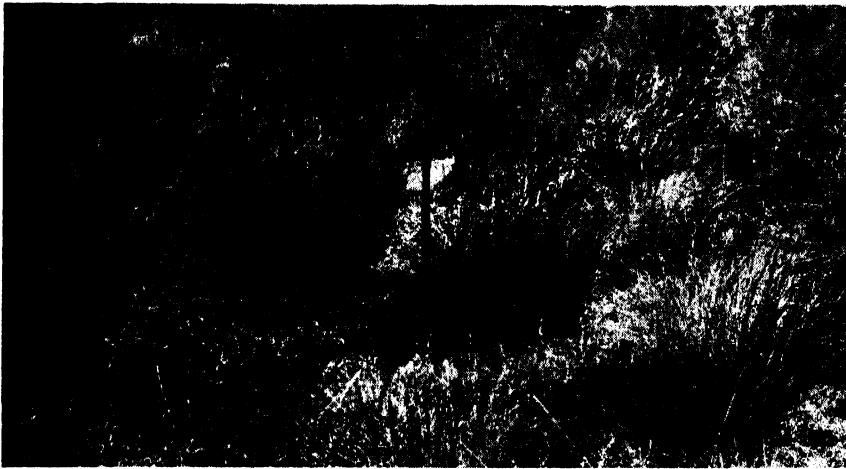


Fɪɢ. 1. Station 1. An area which was lightly grazed prior to 1911, and which is apparently typical of the association in virgin condition. The dominant *Agropyron* bunches contribute 85 per cent of the annual forage output in this community, with the smaller interstitial plants of *Bromus* and *Poa* each contributing 5 per cent. The stake is marked off into decimeter units. All four pictures were taken on May 21, 1938.
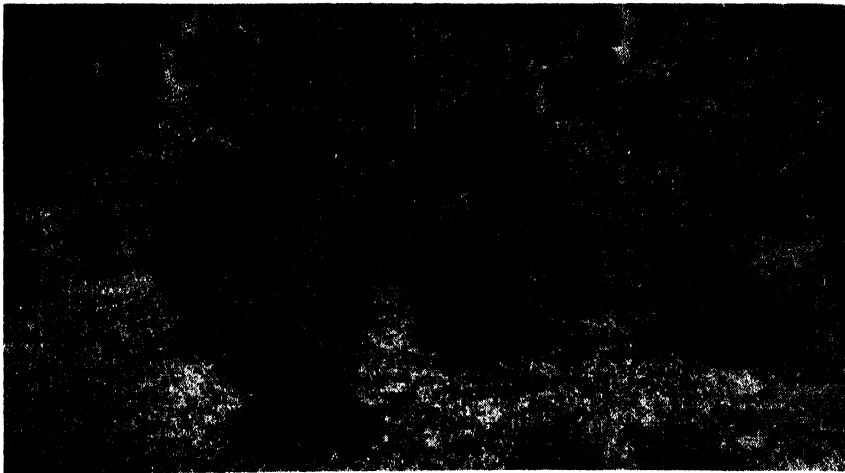


Fɪɢ. 2. Station 2. Heavy grazing has eliminated the smallest *Agropyron* bunches and reduced the size of those remaining. The ground is developing a cover of small plants, part of which are annuals and part perennials.
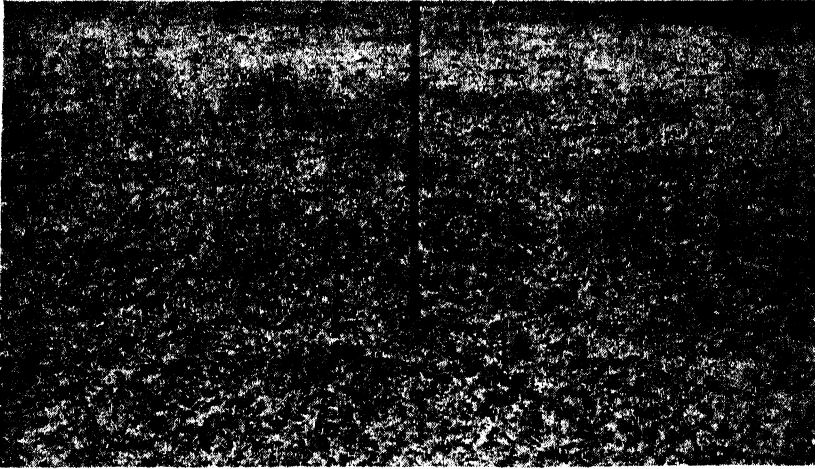
FIG. 3. Station 3. *Agropyron* bunches are eaten back to the ground line so that the short weak shoots which are put forth each year can be distinguished only with close study.
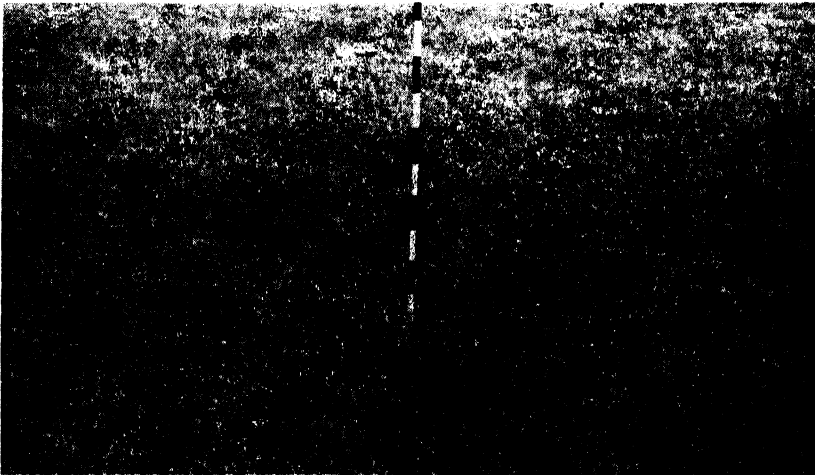


FIG. 4. Station 4. *Agropyron* is completely eliminated here, but the soil is fairly well covered with a community of small unpalatable plants which is dominated by the perennial *Poa secunda* and a group of annual dicots—apparently a biotic climax.

dm. in dimensions, and were arranged in five parallel rows one meter apart. Each plot of the 400 was studied at three critical dates (April 7 or 8, April 30 or May 1, and May 21 or 22) which were so timed on a basis of previous observations that the entire vascular flora (part of which is very ephemeral) could be studied.

## RESULTS

In table III the species encountered in all 400 plots are classified into four groups. Group one includes those species which decrease in abundance as the intensity of grazing increases. This decrease in some if not most cases seems directly due to stock eating the aerial shoots. In perennials, such as *Agropyron*, the underground organs become weakened due to undernourishment caused by the repeated removal of photosynthetic tissue, and the decline in vigor of such plants is gradual until the plant succumbs. With an annual which is grazed, such as

*Bromus tectorum,* the first few years during which the stock feed on the plants so heavily that no seeds are matured spell a rather sudden extinction of these plants from the range. Scattered groups and individuals of *Bromus* seem to escape grazing and smut epidemic each year and these mature a few seeds which are scattered somewhat by the sheep, perpetuating the species in a very thin population.

In this same group there may be other causes for the disappearance of the plants. Some of those species which are not grazed, such as *Lithospermum,* may owe

TABLE III.    *Frequency of plants as affected by grazing. Presence in the community, although not frequent enough to have been included in one of the plots, is indicated by +*

| Behavior under influence of heavy grazing | Species | Per cent frequency of occurrence | | | | Annual (aa) or perennial (p) |
|---|---|---|---|---|---|---|
| | | Climatic climax | Early re-trogr. | Late re-trogr. | Biotic climax | |
| Decreasing in Frequency | *Agropyron spicatum* (Pursh) Scribn. & Smith *.... | 70 | 53 | 22 | + | p |
| | *Bromus tectorum* L................................ | 100 | 3 | 31 | 2 | aa |
| | *Gayophytum ramosissimum* T. & G.†............. | 58 | 17 | 4 | | aa |
| | *Agoseris heterophylla* (Nutt.) Greene............ | 16 | 9 | 9 | 10 | p |
| | *Achillea lanulosa* Nutt......................... | 6 | 3 | + | + | p |
| | *Calochortus macrocarpus* Dougl................. | 4 | | | | p |
| | *Lomatium macrocarpum* (Nutt.) C. & R.......... | 3 | 6 | | | p |
| | *Astragalus spaldingii* Gray..................... | 2 | | | + | p |
| | *Erodium cicutarium* (L.) L'Her................. | 1 | + | + | | aa |
| | *Gilia gracilis* Hook............................ | 1 | | | | aa |
| | *Lagophylla ramosissima* Nut.................... | 1 | | | | aa |
| | *Festuca idahoensis* Elmer...................... | + | + | | | p |
| | *Lomatium triternatum* (Pursh) C. & R.......... | + | + | 1 | | p |
| | *Sisymbrium longipedicellatum* Fourn............. | 1 | | | | aa |
| | *Lithospermum ruderale* Dougl.................. | + | | | | p |
| Increasing in Frequency | *Plantago purshii* Nutt......................... | 84 | 100 | 100 | 100 | aa |
| | *Plagiobothrys tenellus* (Nutt.) Gray............ | 12 | 2 | 28 | 100 | aa |
| | *Cryptanthe flaccida* (Dougl.) Greene........... | | 53 | 56 | 100 | aa |
| | *Pectocarya penicillata* (H. & A.) A. DC......... | | | | 79 | aa |
| | *Lepidium densiflorum* var. *elongatum* (Rydb.) Thell. | | | | 67 | aa |
| | *Lappula redowskii* (Hornem.) Greene........... | 1 | | | 32 | aa |
| | *Erigeron concinnus* (H. & A.) T. & G........... | | | | 30 | p |
| | *Antennaria dimorpha* (Nutt.) T. & G........... | + | 3 | 2 | 8 | p |
| | *Agoseris glauca* (Pursh) Steud................. | 1 | + | 2 | 6 | p |
| | *Stephanomeria paniculata* Nutt................ | | | | 2 | aa |
| Apparently Characteristic of Intermediate Stages | *Lithophragma bulbifera* Rydb.................. | 25 | 98 | 100 | 36 | p |
| | *Festuca pacifica* Piper........................ | 63 | 100 | 70 | 8 | aa |
| | *Alchemilla occidentalis* Nutt.................. | | 79 | 69 | | aa |
| | *Sisymbrium altissimum* L..................... | | 2 | 61 | 2 | aa |
| | *Lomatium farinosum* (Hook.) C. & R........... | | 27 | 2 | | p |
| | *Madia exigua* (Sm.) Gray.................... | + | 32 | | | aa |
| | *Delphinium nelsoni* Greene.................... | | 2 | + | | p |
| | *Ranunculus glaberrimus* Hook................. | | 1 | 2 | | p |
| Frequency Scarcely Affected | *Poa secunda* Presl............................ | 99 | 100 | 100 | 100 | p |
| | *Draba verna* L............................... | 100 | 100 | 100 | 100 | aa |
| | *Brodiaea douglasii* Wats...................... | 21 | | 66 | 23 | p |
| | mosses (all *Bryales*)......................... | 99 | 100 | 100 | 100 | p |

* Includes *A. inerme* (Scribn. & Smith) Ryd. which is considered by the writer as one form of *A. spicatum* (Daubenmire, '39). All have identical ecology in our region.

† This species and *Epilobium paniculatum* Nutt. cannot be distinguished by vegetative structures, and since very few of the plants flower, both species have been lumped under the name of the one which seems to be the most abundant.

their extinction to trampling. Still others may have a more remote cause for decadence, namely, the removal of protection afforded by the larger and more palatable plants. That this can be a potent factor is well shown by the great reduction in stature of *Poa* in the biotic climax (or even in the spaces between the *Agropyron* bunches in the climatic climax) as compared to specimens close up under *Agropyron* bunches. Those in the latter situation are from 50 to 100 per cent taller, apparently due to the protection from insolation and desiccating winds which the tall plants afford.

It is significant from the standpoint of range management that 90 per cent by dry weight, of the total annual output of shoots in the *Agropyron* bunchgrass association is produced by two members of this group of species (*Agropyron* 85 per cent and *Bromus* 5 per cent). The amount of this forage available in the biotic climax is negligible.

A second group contains those species which seem to be favored by grazing. These plants for the most part are not palatable (except for the basal leaves of *Lepidium* and *Agoseris* and small amounts of the young shoots of *Cryptanthe*), are not seriously injured by trampling, and their shoots can withstand exposure to the full force of drying winds and intense insolation. Apparently these species are kept out of the climatic climax by the competition afforded by the dominants of that community. This competitive influence of other plants seems more detrimental to these species than the influence of the animals.

Most of the plants in this group are small annuals, and members of the Boraginaceae are conspicuous among them. Some may be avoided because they are woolly (*Plantago*), others because they are hispid (*Lappula*) or otherwise distasteful to stock. Certain of them may escape only because their foliage appears at the same time as that of a more desirable species. In the case of *Festuca pacifica* the foliage is extremely scanty

and the stems wiry. Obviously these plants make up most of the biotic climax.

A third group of species is made up of plants which appear to be immediately benefited by the removal of the competitive influence of the climatic climax dominants, but which are not very well adapted to the biotic and aerial factors which accompany the final stages of range deterioration. The conditions which favored group two also favor this group during the early stages of overgrazing, but some or all of the factors which operate against group one finally come into play so that these plants are ultimately eliminated. Most of these species are primarily seral, being practically without representation in either climax.

The fourth and last category is an assemblage of hardy unpalatable plants whose abundance seems scarcely increased or reduced by the radical changes in biotic and aerial factors which are brought about by intense grazing. All were present in the climatic climax, have persisted throughout the period of deterioration, and are important members of the biotic climax.

One plant in this last group, *Poa secunda*, deserves special mention. This bluegrass forms about 5 per cent of the total shoots (by dry weight) produced annually by the vegetation under climatic climax conditions. The forage value of this species over most of its range is rated as fair, and the average height is about 3 dm. (U. S. D. A. For. Ser., '37). As the protective influence of the larger plants in our region is removed, the stature of *Poa* decreases until the plant is considerably below this average, and the leaves become so fine and wiry that they are scarcely ever eaten by any class of livestock. Undoubtedly the nature of this plant's response to the removal of the larger and more palatable *Agropyron* is the key factor in its persistence into the biotic climax. The climate of this region, with its extremely dry summers, probably emphasizes this phenomenon.

From the foregoing it is evident that

plant succession leads from the climatic climax of *Agropyron-Poa-Bromus* to a biotic climax dominated by *Poa* and small annual dicots among which members of the Boraginaceae are conspicuous. This process is not marked into recognizable stages. Animal influence results in bare areas only where trampling is excessive, such as around a corral or bedding ground.

Since *Agropyron* and *Bromus* together form 90 per cent of the climatic climax vegetation and nearly 100 per cent of the valuable forage, any plan of range management which maintains the vegetation in a condition most nearly approximating the virgin state would be most desirable. Although no extensive study has yet been attempted to determine the most appropriate grazing system in this region, some observations by the writer are significant in this connection.

Several clipping experiments were made in eastern Franklin County. When *Agropyron* was clipped to the ground at the height of its growing season in late spring, most of the clipped plants succumbed, and the next year the few survivors produced only small tufts of foliage with no inflorescences. On the other hand, grazing the *Agropyron* bunches to the ground

during the summer and fall appears to have only slight detrimental influence upon the plants. The writer has observed a fence-corner relic of this association in Whitman County, which has remained in fair condition despite the fact that live-stock which are turned into the field after the wheat is harvested often graze the *Agropyron* to the ground during this period of vegetational aestivation (figs. 5 and 6). These observations indicate that a desirable grazing system would emphasize fall or winter utilization of cured shoots and minimize spring use of the range.

In another experiment, single bunches of *Agropyron* were released from the competition afforded by surrounding plants by keeping the latter clipped to the ground. The experimental plants showed no great response the subsequent season, but by the third year the increase in size and vigor was very apparent, so that it may be concluded that competition checks the stature of even the most dominant plants in the association.

Within the areas where *Agropyron* was practically eliminated by clipping, some of the annuals, chiefly *Bromus, Erodium, Lagophylla, Plagiobothrys* and *Sisymbrium longipedicellatum* showed increase
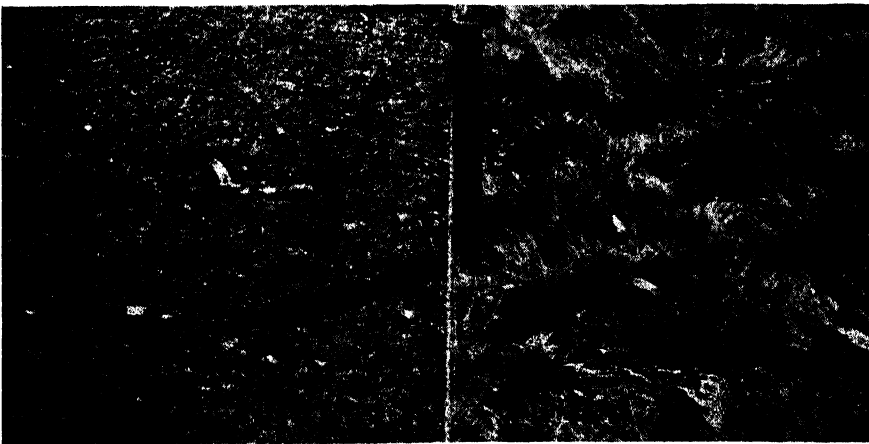


FIG. 5. Whitman County, Washington, April 7. *Agropyron* in the pasture to the left of the fence was grazed to the ground during the preceding autumn. Near-virgin prairie to the right of fence. The soil here is about a meter deep; the stones on the surface were thrown there incidental to the excavation of a deep road cut to the right of the photograph.
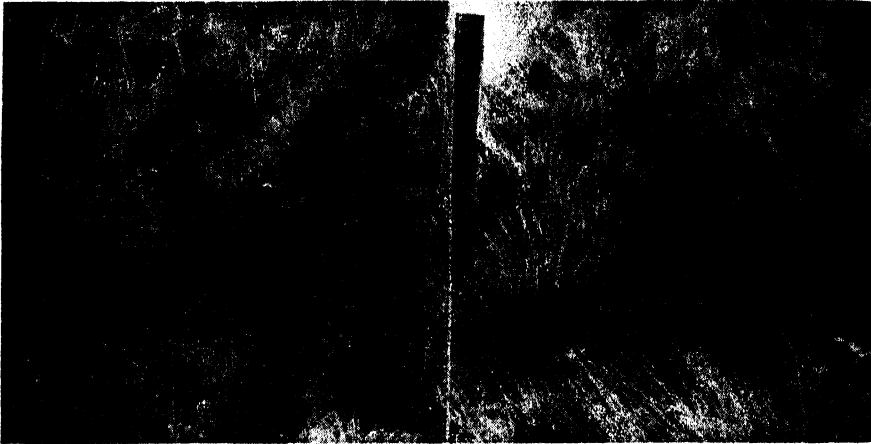
FIG. 6. Photograph of the same area shown in figure 5, taken on May 21 after the *Agropyron* within the pasture had attained nearly the size of the ungrazed plants to the right of the fence. The bunches outside the fence are denser and lighter in color due to the presence of old bleached shoots. *Sisymbrium altissimum* is conspicuous within the pasture.

in size the first year, and increase in numbers on subsequent years. *Lappula* has a strong tendency to invade these clipped areas.

These clipping experiments show that there is considerable competition among the dominant plants (*Agropyron* bunches) as well as between them and the subordinate annuals. When *Agropyron* is weakened or destroyed by injury during its period of active growth, the lessening of competition allows the annual flora to expand so that the ground surface remains well covered. Although valueless as forage, these plants of the biotic climax have distinct value as soil binders in as much as they are fairly efficient in retarding erosion of the topsoil.

## DISCUSSION

The above studies, together with other observations by the writer, bring out the fact that the ecologic responses of several plants in Washington are different from their responses to grazing in other parts of the western United States, as indicated by the literature. Four plants deserve special mention in this connection: *Salsola kali* L., *Bromus tectorum*, *Agropyron spicatum*, and *Artemisia tridentata* Nutt.

In the recent summary of range conditions in the western United States (U. S. D. A. For. Serv., '36), some general references are made to the behavior of these plants in regions where *Agropyron spicatum* is dominant. These references seem to be based on researches in the regions to the south and east of Washington since no previous study of grazing succession in this state has appeared. It will be evident from the following discussion that in Washington, which includes only a small part of the total *Agropyron* rangeland, conditions apparently exist which are not typical for the range as a whole.

*Salsola*, this source states, is widely distributed in some parts of the bunchgrass range. In our particular region it is closely confined to road right-of-ways, and seems wholly incapable of invading virgin or grazed pastures in this prairie type.

*Bromus tectorum*, this account also remarks, "is now dominating large areas formerly occupied by bunchgrass." This is true in Washington, but the statement needs qualification here. *Bromus* does not dominate ranges which are being heavily grazed during the spring season. When, after heavy grazing, herbivore

pressure is reduced, *Bromus* quickly dominates the area, the other species of the climax entering much later. Patches where the density of this plant is very high occur throughout all grazed areas in this region. These may possibly be explained by a lack of uniformity in spring grazing, coupled with the readiness with which the species will enter grazed lands. If on two or more successive years, a given area escaped grazing during the short vernal season when *Bromus* is highly palatable, this grass would undoubtedly dominate the area. These island-like patches of *Bromus* increase in abundance with distance from watering places, a fact which is in harmony with this explanation of their existence. That the *Bromus* colonies are not the simple and direct result of overgrazing is indicated by the extensive gaps between the colonies, which gaps are heavily used by the sheep. .

Smut infections are not responsible for the interstitital areas because the *Bromus* islands show strong conformity with fences wherever these result in unequal grazing intensity in adjacent pastures.

There also seem to be other factors (perhaps cultivation, fire, etc.) which promote dense stands of this grass, but it is not to be considered here as a species directly favored by overgrazing, for it is highly palatable and is practically eliminated by uniformly heavy spring grazing.

Again, it is stated that in some regions the *Artemisia tridentata* association may enter and dominate an area which before grazing contained little if any of this shrub. This cannot be said for Washington, however, for the writer has seen no evidence of this phenomenon although he has looked for it for three seasons. Communities of *Artemisia tridentata* are common in the region where the present study was made, but these are to be found only on sandy soils of stream terraces and never show the slightest tendency to invade the surrounding finer-textured uplands from which most or all of the bunchgrass has been grazed.

*Agropyron* and *Artemisia* seem to be complementary rather than competitive in central Washington, whereas in southern Idaho the competition between the same species is keen. In parts of the latter region overgrazing tends to result in a pure stand of the shrub, while complete protection from grazing allows the grass to become at least equally as important as the shrub in the climatic climax (Craddock and Forsling, '38).

Any peculiarities which may exist in the behavior of plants in southwestern Washington may possibly be attributed to several peculiarities of the climate in this region. In contrast to regions farther south and east, the climate in this north arm of the Columbia Plateau is characterized by considerably greater cloudiness (Kincer, '22, p. 44) and less insolation (Kincer, '28, p. 33), with a consequence that the average relative humidity at 2 P.M. is higher at all seasons (Kincer, '22, p. 45).

Although the total precipitation is not significantly different between the two portions of the Plateau (Kincer, '22, p. 30), the higher moisture content of the air results in a higher precipitation/evaporation ratio for the frostless season in Washington than in southern Idaho (Livingston and Shreve, '21, p. 342).

Winter temperatures seem also to be influenced by the humid air which blankets this northern region. Judging from the number of days with the minimum temperature below freezing (Kincer, '28, p. 9), the winter temperatures are less severe in Washington than in Oregon and southern Idaho.

These climatic data indicate that sufficient differences in climate may exist to account for different ecologic responses of *Agropyron*, *Artemisia*, and other associated plants, in Washington and in regions farther south.

Association for supporting these studies with a Research Grant, and to Mrs. Daubenmire for valuable assistance in the field.

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# SOME ECOLOGICAL CONDITIONS IN A BRACKISH LAGOON

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In connection with an attempt on the part of a group of anglers to transform a salt-water lagoon into a fresh-water lake for the propagation of trout, a series of observations has been made of the biological conditions existing during the course of the experiment. The body of water known as Lost Lagoon is 60 acres in area and lies at the entrance to Stanley Park, Vancouver, B. C. It was formerly open to the harbor from which it received its water but in 1916 this connection was broken by a highway embankment built across the narrowest portion. Later the lagoon was provided with a small inflow of fresh water from the city supply and with an outlet system with a valve to allow for overflow and at the same time to prevent the entrance of sea water. However, despite the continuous addition of fresh water, the amount of salt in the lagoon has remained appreciable apparently due to a constant seepage of sea water through the embankment and to leakage past the valve in the overflow pipe during periods of high tide in the harbor. As a result, the water has continued to be brackish, the degree depending upon the amounts of fresh water flow, rainfall, leakages, etc. and has supported a community of both marine and fresh-water animals and plants under somewhat rigorous conditions.

In a former publication presenting ecological notes on the flora and fauna of the lagoon (Carl, 1937) mention was made of the death of fish presumably resulting from algal decomposition. In the hope of obtaining records of water conditions during a possible repetition of this phenomenon a program of more intensive study was carried out over a period of two years. Although the death of fish on a large scale did not occur during the period in question, a number of observa-

tions were made and some of the results are embodied in the present paper.

## Technique

As the investigation was concerned with physical and chemical conditions of the water and the relation between them and the planktonic plants and animals, a schedule of regular sample taking was commenced. All water samples were taken at a station as far removed as possible from disturbing factors and at a depth of 12 inches below the surface. Previous investigation had shown that samples taken thus were fairly representative of the lagoon. Plankton samples were obtained by pouring 10 gallons of water taken from the same depth, through a standard-sized net of no. 20 bolting silk. Meteorological data were obtained from the local office of the Dominion Meteorological Service. During the greater part of the observation period, March 1934 to June 1935, samples were taken at fortnightly intervals; during the remaining portion of the period collections were made at less regular intervals. The routine of each analysis included determinations of temperature, pH and dissolved oxygen content which were made in the field and measurements of color, silicate content, nitrates, nitrite, chloride, carbonates (as normal and acid carbonate) and nitrogen content in the form of total organic nitrogen, free ammonia and albuminous material, which were carried out in the laboratory using methods outlined in Standard Water Analysis (1925). The results of this series of analyses are graphically presented in figures 1 to 4.

A few of the tests which usually give good results when applied to salt or fresh water proved quite unsatisfactory when applied to the lagoon water. For example, determination of phosphate by the
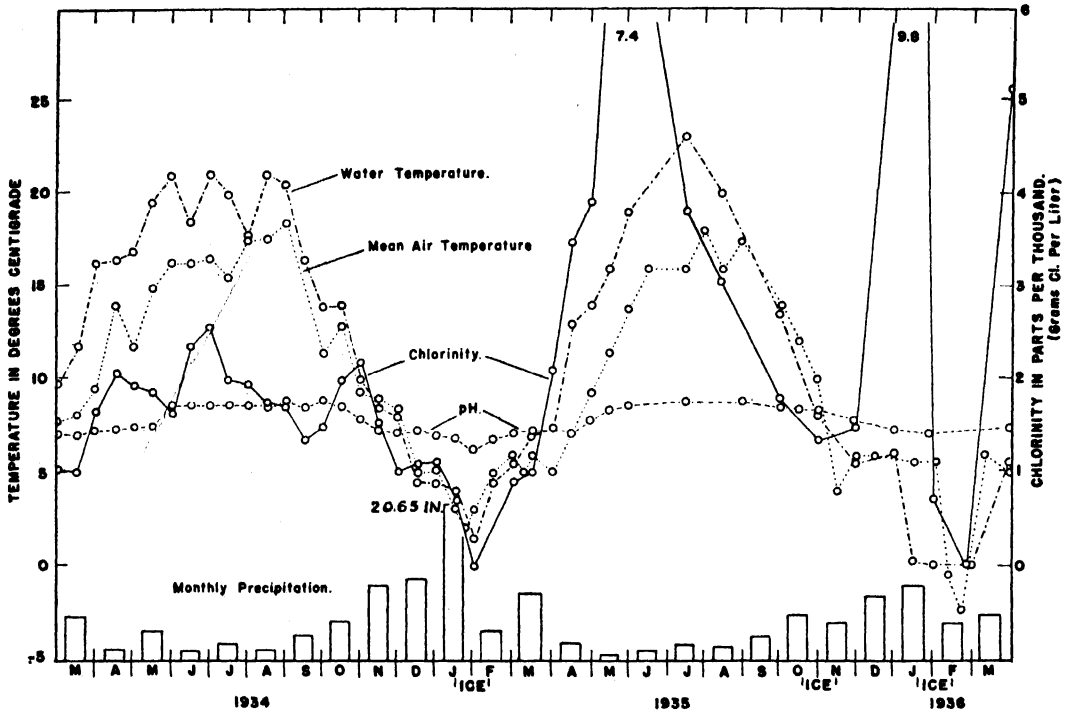
FIG. 1.   Relationships between chlorinity, precipitation and mean temperatures of air and water, Lost Lagoon, March 1934 to March 1936.
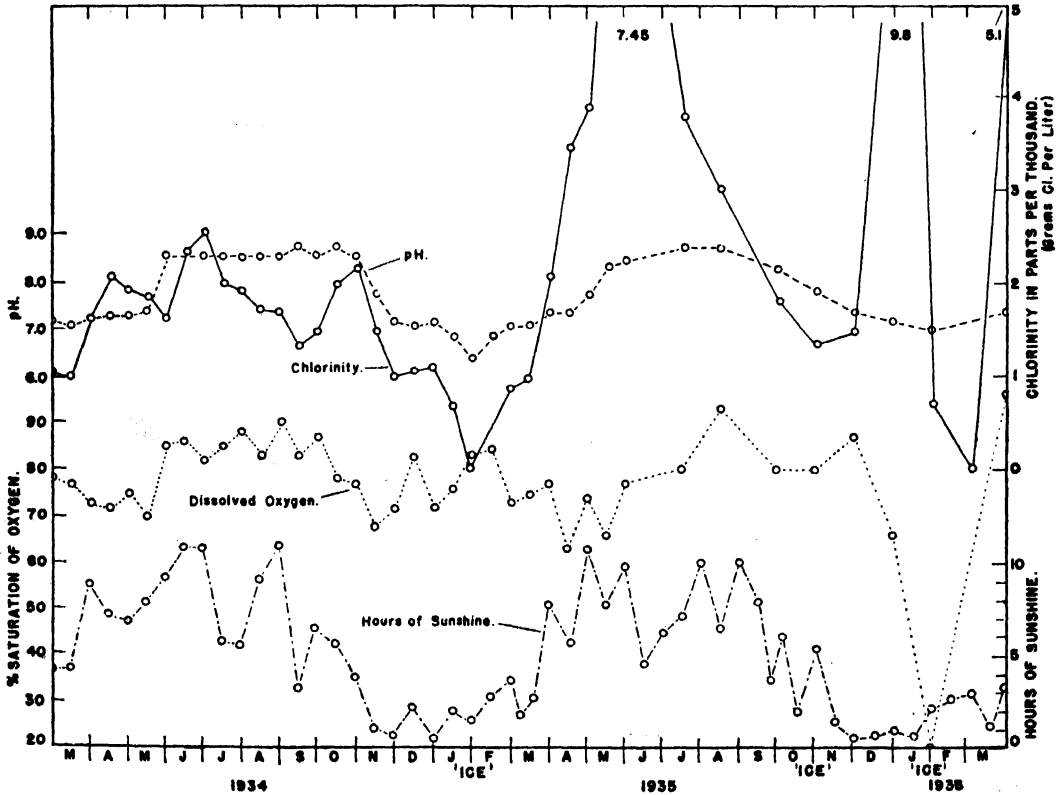


FIG. 2.   Relationships between oxygen saturation, amount of sunlight, hydrogen ion concentration and chlorinity, Lost Lagoon, March 1934 to March 1936.
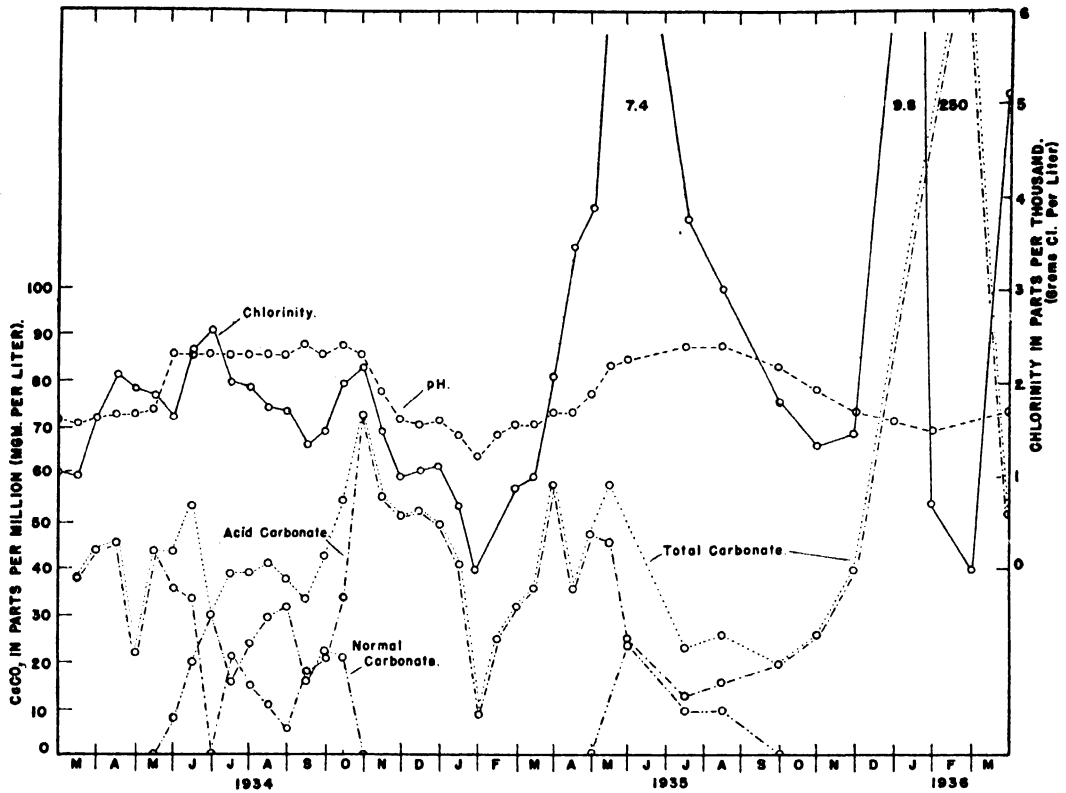
FIG. 3.  Relationships between acid and normal carbonates, chlorinity and alkalinity, Lost Lagoon, March 1934 to March 1936.
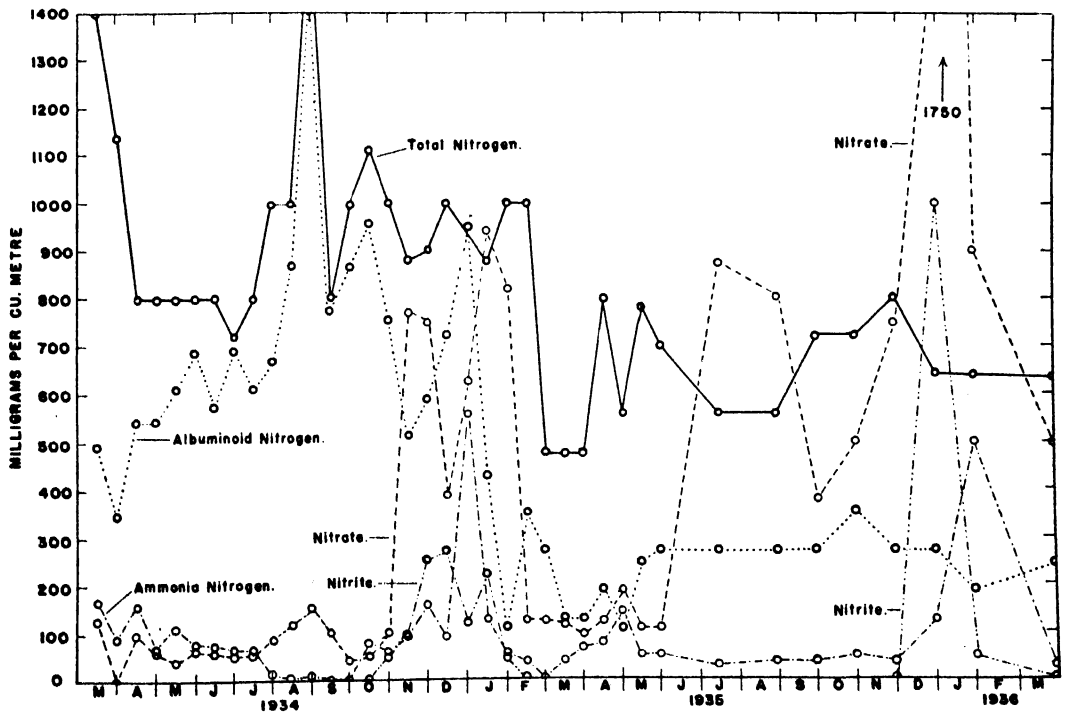


FIG. 4.  Variations in amounts of nitrogen in the form of ammonia, nitrate, nitrite and albuminous material, Lost Lagoon, March 1934 to March 1936.

usual colorimetric method gave unreliable results and was discontinued. Colorimetric analysis of nitrate and nitrite also proved to be unsatisfactory but was continued in the hope of determining the cause of the disturbance. After a number of tests was made it was found that the presence of appreciable quantities of nitrate was detectable only when the amount of albuminous material was low, as shown in figure 4 (Nov. 1934, Jan. and Feb. 1935). This suggests that the presence of a large quantity of particulate organic material which is normally found in the lagoon water, masks the presence of soluble nitrates and other substances such as phosphate, possibly by adsorption of the acid radicles to the surface of the suspended particles and thus preventing their detection by removing them from true solution. At present there appears to be no way of avoiding this difficulty since any attempt to free the adsorbed substances results in their destruction.

## PLANKTON CYCLE

The series of determinations of other substances present in the water of Lost Lagoon produced some results which show general conditions obtaining within the lagoon and indicated certain relationships with the plankton population. The seasonal occurrence and variation in numbers of four major groups of planktonic organisms as obtained by counts made for each sample, have been shown (Carl, 1937, fig. 3). It will be noted that during the first year the monthly distribution of these groups is fairly typical of plankton communities since phytoplankton (diatoms) show a small population peak in early spring followed by zooplankton such as rotifers and copepods with a bloom of blue-green algae (Cyanophyceae) occurring near the end of the summer. The death of this algal crop was followed by an increase in the numbers of rotifers which in turn were supplanted by a rise in diatom population during November and December 1934.

The cycle then commenced in repetition with slight variations in time and numbers of individuals but failed to complete itself after August 1935.

The plankton organisms consisted of both fresh-water and brackish-water species. Diatoms were represented by *Tabellaria fenestrata* Kutz., *Cyclotella meneghiniana* Kutz., *Asterionella formosa* Hass., and *Melosira varians* Ag. of which *Tabellaria* and *Cyclotella* were the most abundant. The blue-green algae consisted chiefly of *Anabaenopsis elenkini* V. V. Miller which occurred as a bloom in the summer of 1933, again in smaller numbers in 1934 and in an almost insignificant amount in 1935. The rotifer fauna included *Keratella cochlearis* var. *tecta* (Gosse), *K. cruciformis* (Thompson), *Notholca striata* Ehrenberg, *Brachionus urceus* Linné, *B. plicatilis* Mobius, *Trichocera* sp. and *Synchaeta* sp. All are fresh-water species except *N. striata* and *B. plicatilis* which are characteristic of brackish water. The population peaks were due to the presence of *K. cruciformis* in 1934 and again in 1935 when this species was associated with *B. plicatilis*. The copepod population was made up mainly of the salt-water parasitic species *Ergasilus turgidus* Fraser (free-swimming males) in 1934 and the brackish-water species *Eurytemora affinis* (Poppe) in 1935. *Nitocra typica* Boeck and *Mesochra rapiens* (Schmeil) both characteristic of waters of low salinity, were also found but in small numbers.

## CHLORINITY

During the period of study the chlorinity of the lagoon water varied considerably being dependent upon several factors. In general, the amount of chloride per litre was greater in the summer during periods of light precipitation and increased evaporation and less in the winter following times of heavy precipitation as indicated in figure 1. This trend, however, was disturbed on several occasions during 1935–36 when salinity values were

found to be greatly in excess of those obtaining in 1934.

The effect of increased chlorinity upon plankton production may be seen by comparing the plankton cycle (Carl, '37, fig. 3) with water conditions as shown in figure 1 for the year 1935. It may be noted that following the first greatly pronounced rise in chlorinity to 7.45 gms. of Cl per litre during May and June 1935 the freshwater phytoplankton almost completely disappeared while the brackish-water zooplankton represented by the rotifers K. cruciformis and B. plicatilis and the copepod E. affinis, increased in quantity. Following the second and greatest rise in chlorinity to 9.8 gms. per litre in December 1935 and a lesser rise in March 1936 the plankton population showed no signs of returning to its former numbers. Investigation revealed that these abnormal rises in chlorinity were due to the presence of large quantities of sea water which were allowed to enter by way of the overflow pipe.

## OXYGEN

The amount of oxygen dissolved in the lagoon water also appeared to vary considerably. In general, values were high during the summer months (maximum 90 per cent saturation) and lowest during the winter months (minimum 0 per cent saturation in certain small areas) as shown in figure 2. The amount of oxygen appears to be correlated roughly with the amount of sunshine as shown in the same figure but it does not seem to be correlated with the amount of plankton present as indicated by comparison with the plankton cycle (Carl, '37, fig. 3). Thus, it will be seen that the greatest oxygen values do not coincide with times of phytoplankton abundance. For example, during September, October and November 1934, when diatoms and blue-green algae were present in large numbers oxygen values were not as great as during June, July and August when phytoplankton was practically absent.

However, in the summer months rooted aquatic plants such as Ruppia maritima and unattached filamentous algae such as Spirogyra were abundant and were probably responsible to a large extent for the maximum oxygen values obtained at that time. Wind action may also have been a factor but this was not measured.

The general lowering of dissolved oxygen content during April and May, 1935, seemed to be produced by the death of the alga Spirogyra possibly as a result of the increased salinity. Tests at that time gave a minimum of 66 per cent saturation at the sampling station while small areas in the vicinity of decaying algae along the shore were found to be practically depleted of dissolved oxygen. Later in the period of observation (January, 1936) oxygen was entirely lacking at the sampling station a few days after an ice cover had formed. This condition also appeared to be the result of the decomposition of plant material but was no doubt aggravated by the presence of the covering of ice which prevented the absorption of oxygen from the air. Although fish were known to be present in the lagoon no signs of death by asphyxia were observed.

## AIR AND WATER TEMPERATURES

The effect of mean air temperatures upon water temperature and the relation of temperature to plankton production may also be noted particularly during the first half of the observational period (fig. 1). It appears that water temperatures were higher than mean air temperatures during the summer months but were lower than air temperatures for short periods in the winter and that diatoms flourished during periods of low temperature while blue-green algae appeared only following a period of high temperature in August and September, 1934.

## CARBONATE CONTENT

The picture is further complicated when changes in the carbonate content of

the water over the same period of time are included as shown in figure 3. From this graph it appears that the total carbonate content varied directly as the chlorinity since the maxima and minima of the two coincided to some degree. This leads to the conclusion that the carbonate content of the lagoon water is dependent upon the presence of sea water which provides the calcium necessary for the production of carbonate by combination with carbon dioxide.

During the greater part of the year the carbonates were in the acid form $(Ca(HCO_3)_2)$ but during the summer months part of the carbonate was in the normal form $(CaCO_3)$ and on one occasion all the carbonate was in this form (June, 1934). When normal carbonate was present the alkalinity of the water was greatest as indicated by pH readings, a relationship which is evident in figure 3. During these periods the animal complement of the plankton was low as is shown by comparison with the plankton cycle (Carl, '37, fig. 3). This suggests that in times of abundant zooplankton carbonates were transformed to the acid form possibly by the production of $CO_2$ in respiration.

## HYDROGEN ION CONCENTRATION

The hydrogen ion concentration seems to be dependent partly upon the type of plankton organism present and partly upon the chlorinity or carbonate content of the water, since the pH values are highest during blooms of phytoplankton and at times of increased chlorinity and lowest when phytoplankton is small in amount and when the chlorinity is decreased. A relation between pH, percentage of dissolved oxygen and amount of sunshine (shown as average number of hours per day during each fortnightly period, figure 2) is also evident but no single factor controlling the hydrogen ion concentration is apparent from these illustrations.

## NITROGEN CONTENT

The amounts of nitrogen present in the lagoon water in the form of ammonia, nitrate, nitrite and albuminous material showed considerable variation 'throughout the investigational period as indicated in figure 4. The ammonium nitrogen content was low, being less than 170 mgs. per cu. metre except in December, 1934, and January, 1936, at which times it reached 560 and 500 mgs. per cu. metre respectively. In general, albuminoid nitrogen was high during 1934 and low for the remainder of the period of investigation. The increases in amounts of albuminous material indicated by peaks in the graph seemed to follow periods of abundance of plankton organisms, suggesting that the source of the nitrogenous matter may have been the decomposing plankton element. The graph of the values for the total nitrogen content shows somewhat the same relationship.

The presence of nitrite was detected only in the winter months, namely from November to February in each year. This does not necessarily mean that nitrite was absent at other times of the year but rather that the change from ammonia to nitrate was being carried on too rapidly to allow the detection of the intermediate stage.

Since the values for nitrate content appear to be in error for the reasons given in a foregoing section, they will not be considered.

## POLYGONAL PRESENTATION

In the illustrations of the foregoing section the seasonal changes in a few related factors are clearly indicated in each graph but the relationship between each of several factors, and the effect on one of changes in others is not clearly seen. When many factors are involved and the usual method of presentation is unsatisfactory the system of polygonal presentation as developed and demonstrated by Hutchinson ('36) sometimes proves useful. Accordingly, to illustrate more
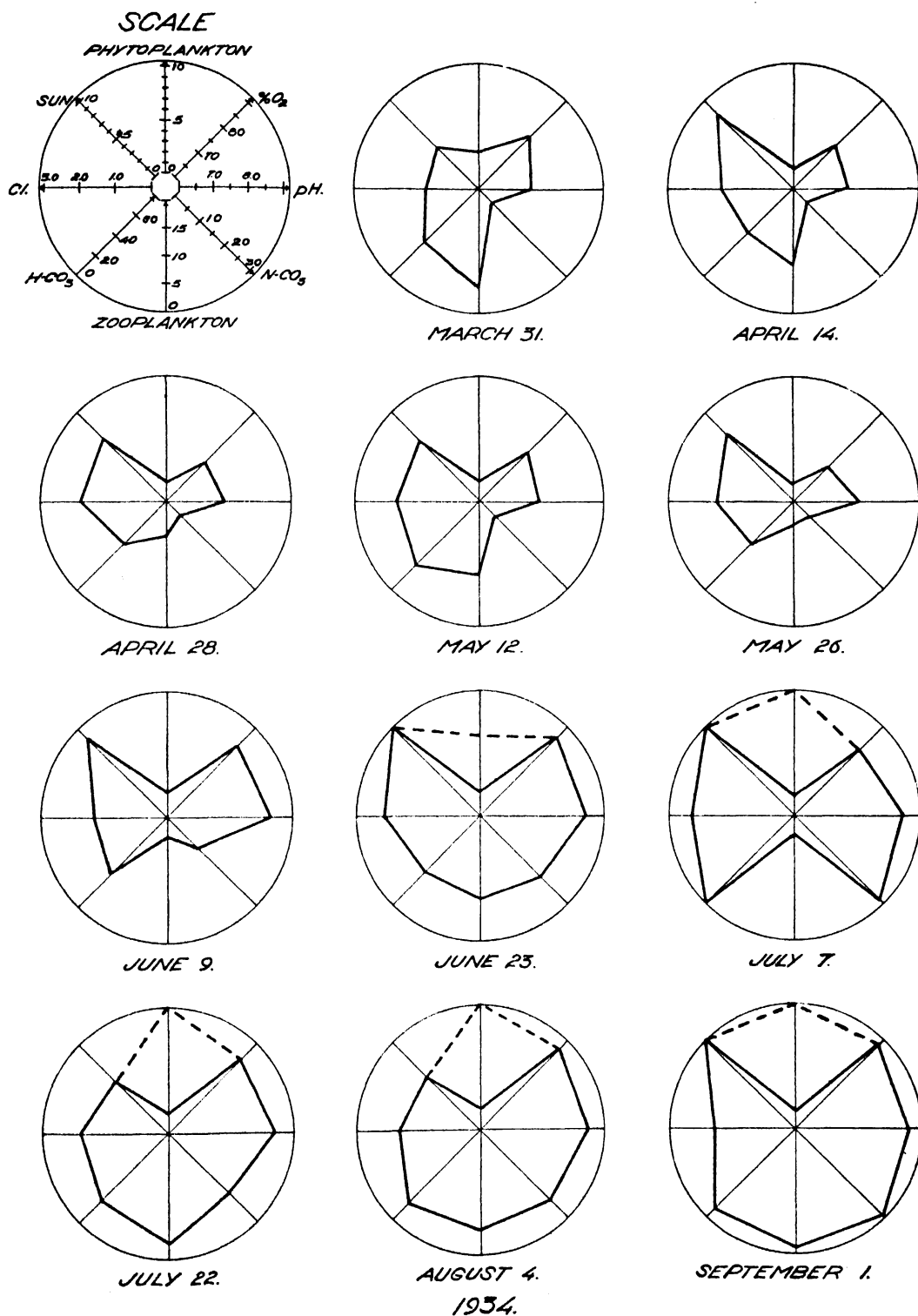
FIG. 5. Relationships between the amounts of phyto- and zooplankton, dissolved oxygen, pH, normal and acid carbonates, chlorinity and sunshine in Lost Lagoon from March 31 to September 1, 1934.
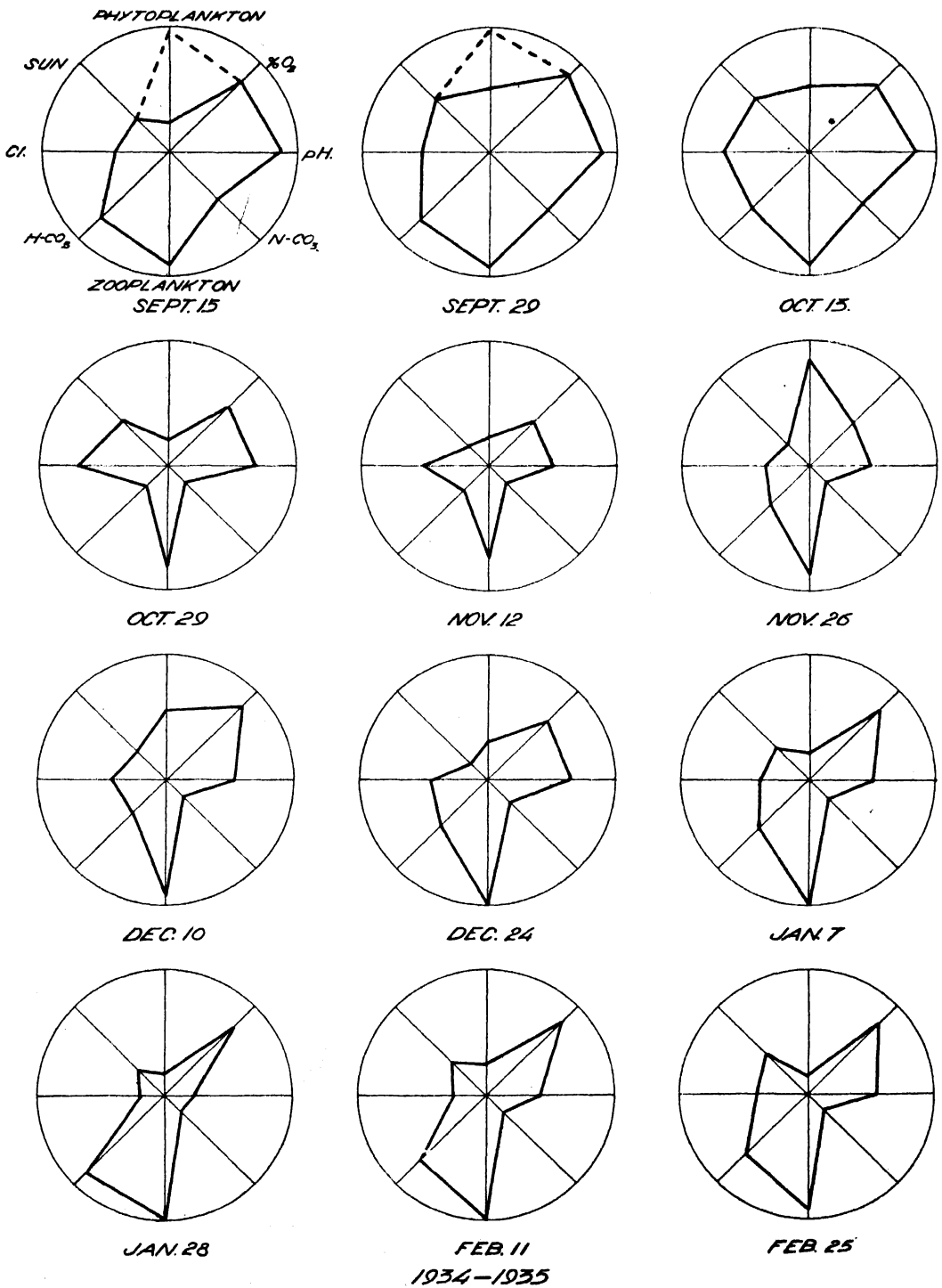
FIG. 6. Relationships between the amounts of phyto- and zooplankton, dissolved oxygen, pH, normal and acid carbonates, chlorinity and sunshine in Lost Lagoon from September 15, 1934 to February 25, 1935.

clearly the relationships which are seen only with difficulty in figures 1 to 4, a portion of the same data is presented in the polygonal system in figures 5 and 6. The factors demonstrated include the amounts of phytoplankton and zooplankton (shown as thousands of organisms per gallon), the amount of dissolved oxygen (per cent saturation), the hydrogen ion concentration (pH), the amounts of normal and acid carbonate (given as parts per million of $CaCO_3$), the salinity (shown as gms. Cl per litre) and the amount of sunlight (shown as the daily average number of hours for the fortnight period).

Each factor is plotted along the radius of an octagon with the zero point either near the centre or on the periphery according to whether the fluctuations in the factor are negative or positive as compared with the other factors and the plotted points on each radius are connected by lines to form an eight-sided figure. It has been shown by Hutchinson that when a series of these figures is prepared using related factors, the shape of the polygon will change in a regular manner and that a specific shape will be indicative of a certain set of conditions. Thus, in figures 5 and 6 it will be seen that as the season progressed the figure changed from an irregular form on March 31 to a more regular polygon during the summer and back to an asymmetrical form during the winter months. The elongated figure roughly approaching a triangle in shape as shown for January and February represents the static condition when animal and plant activities are at a minimum. At this time the dissolved oxygen content is fairly high being more or less undisturbed by biological processes. The contraction of the figure, as shown for April and May, indicates increased animal activity (respiration) with the utilization of part of the dissolved oxygen, production of acid carbonate and lowering of pH values. The expansion of the figure, as shown for July, August and September, represents increased plant activity (photosynthesis) with production of dissolved oxygen, normal carbonate and augmented pH values. The broken lines in the figure for this period represent the presence of abundant rooted aquatic plants which are probably responsible for the greater part of the photosynthetic activity.

In addition to these general tendencies which are illustrated by this series of figures the effect of changes in individual factors is also noticeable. For example, an increase in chlorinity by addition of sea water or by evaporation, produces an expansion of the figure along the pH and normal carbonate radii. The increased activity of calcium precipitating organisms such as molluscs causes similar changes in shape. An increased amount of sunlight causes an expansion of the figure along several radii, notably those representing oxygen saturation, pH, normal carbonate and phytoplankton (including rooted aquatic plants). Similar effects may be noted for other factors.

SUMMARY

1. Over a period of two years (March 1934–March 1936) a series of water and plankton samples was taken to determine the ecological conditions in a brackish-water lagoon.

2. The plankton cycle was found to be typical of fresh water communities in

general during the first part of the season but was seriously disturbed during the remainder of the investigational period by the influx of sea water. The plankton population was composed of both fresh-water and brackish-water organisms and in addition, one species of salt-water parasitic copepod.

3. The chlorinity of the water was greater in summer and less in winter in 1934, the variation no doubt being related to the amount of precipitation. It was abnormally high in 1935–36 due to the presence of large quantities of sea water. Following the first pronounced rise in chlorinity, fresh-water phytoplankton decreased and brackish-water zooplankton increased in numbers but following still greater rises in salinity the plankton population was reduced to an almost insignificant amount.

4. The amount of dissolved oxygen seemed to be correlated with the amount of sunlight through the photosynthetic activities of phytoplankton and larger aquatic plants but a complete lack obtained on one occasion in small areas near decaying algae along the shore and later under an ice cover at the sampling station.

5. Water temperatures were higher than mean air temperatures in summer but lower for short periods in winter.

Diatoms occurred during periods of low water temperature in the spring and fall but blue-green algae appeared after a period of high temperature.

6. The total carbonate content appeared to vary directly as the chlorinity. Carbonates were detected in the normal form in summer only, when the animal component of the plankton was low.

7. The hydrogen ion concentration seemed to be influenced partly by the type of plankton organism present and partly by the chlorinity and carbonate content of the water.

8. The ammonia nitrogen content was low in general while the albuminoid nitrogen content was high and the increased amounts of nitrogenous matter as found on several occasions may have been produced by the death of the plankton crop. The presence of nitrite was detected only in the winter possibly because oxidizing processes are slowed down at that time.

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# ECOLOGICAL ASPECTS OF LONGLEAF PINE REGENERA-TION IN SOUTH MISSISSIPPI

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Prompt natural regeneration of desirable tree species is the aim and desire of all foresters and landowners who plan to grow continuous crops of timber. Success is not always achieved, however, especially in the case of longleaf pine (*Pinus palustris*), reproduction of which has proved to be an extremely complex ecological problem.

This paper deals with the results of a series of experiments on (1) protection of longleaf pine seed and seedlings from birds and rodents before and during germination, and (2) the preparation of seedbeds to insure prompt and complete germination and satisfactory initial establishment of longleaf pine. The experimental work was conducted in 1935 and 1936 at the Harrison Experimental Forest in southern Mississippi. Field work was done principally on small plots on cut-over pine lands characterized by scattered seed trees and a heavy grass rough.[2] Laboratory work was carried on in a greenhouse in small sand and soil flats. Each test was arranged and replicated so that the results could be subjected to analysis of variance, and differences discussed in the following pages are statistically significant unless otherwise qualified.

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[1] Formerly with the Southern Forest Experiment Station, now Associate Forester, Intermountain Forest and Range Experiment Station.

[2] Rough is a term widely used in the South to denote the accumulated living and dead grasses, weeds, and brush that make up the ground cover in southern forests. The term is used here in a more restricted sense and denotes principally the upper portion of the ground cover, which is composed of a tangled mass of dead and living vegetation in a more or less upright position or partially suspended above the soil surface. The exact composition and structure of the rough will vary with the forest cover with which it is associated.

## PROTECTION OF SEED AND SEEDLINGS

The major purpose of these studies was to determine the effects of different seedbed conditions, forest-cover types, mulches, and methods and seasons of sowing—alone and in different combinations—on the establishment of longleaf pine reproduction.

*Surface Treatment and Method of Sowing.*—The first study consisted of a series of direct sowings in which three seedbed conditions, four methods of sowing, and two seasons of sowing were used. The seedbed conditions were: (1) undisturbed soil and grass rough, (2) soil from which the rough had been removed by broadcast burning, and (3) cultivated soil. The sowing methods consisted of (1) placing three seeds together at 1-foot intervals on top of the soil, (2) covering similarly sown seed with a mulch of grass, (3) drill sowing with a hand-operated seed drill, and (4) sowing seed inside of small wire tubes set upright in the soil. A first sowing was made in November 1935, and a second in January 1936. In all, 1488 spots were under observation, in each of which equal quantities of seed were used.

Table I shows that in the autumn the three methods involving protection of the seed gave on the average better results than ordinary surface sowing. The wire-tube method was outstandingly successful in the winter, when mulched and surface-sown seed were completely destroyed by birds and rodents. Of the various combinations of sowing method and surface treatment used in the autumn, drill-sowed and burned, mulched and cultivated, and the use of wire tubes in the rough were by far the best. The wire tubes in cultivated soil, and surface sowing on burned soil, gave the poorest results. The tubes

TABLE I. *Mean per cent of successful spots,[3] by sowing and treatment*

| Method of sowing | Treatment | | | Sowing mean |
|---|---|---|---|---|
| | Culti-vated | Rough | Burned | |

*Autumn sowing, November 1935, tallied April 2, 1936*

| | | | | |
|---|---|---|---|---|
| In tubes | 23.3 | 74.3 | 40.0 | 45.9 |
| Mulched | 76.3 | 32.3 | 57.7 | 55.5 |
| Drilled | 41.0 | 36.0 | 82.0 | 53.0 |
| On surface | 32.0 | 31.3 | 3.7 | 22.3 |
| Treatment mean: | 43.2 | 43.5 | 45.8 | 44.2 |

*Winter sowing, January 1936, tallied April 2, 1936*

| | | | | |
|---|---|---|---|---|
| In tubes | 68.3 | 91.7 | 81.0 | 80.4 |
| Mulched | 0 | 0 | 0 | 0 |
| Drilled | 32.0 | 1.0 | 50.7 | 27.9 |
| On surface | 0 | 0 | 0 | 0 |
| Treatment mean: | 25.1 | 23.2 | 32.9 | 27.1 |

in the rough were unusually successful in the winter sowing, although the other tube and surface combinations were noticeably successful. Seed sown in drill on the two surfaces free of debris also gave commendable results.

Failure to get consistent results within a given surface treatment is due to interaction with the seeding method. Cultivated soils failed largely because of a tendency for the soil to silt over the seed and seedlings. In the case of the rough surface, the tube method was the only one in which the seed was sown in mineral soil; the drill sower in particular failed to properly sow seed on this surface. On the burned surfaces, both drill and tube sowings hid the seed from the eyes of birds and rodents, but ash and debris washed in by heavy rains silted over the seedlings and tended to clog the tubes.

*Mulches.*—Further evidence of the protective value of mulches was obtained in connection with the direct seeding of

[3] At least one seedling per spot was classed as successful.

an area of 2½ acres a short distance from the foregoing tests. Following the complete loss of a surface sowing of longleaf pine seed on a recent burn, three types of protective mulch were tried: heavy hay mulch, light hay mulch, and a light pine straw cover, all applied December 20–21, 1935. One ounce of seed was sown on each of 225 milacre quadrats, and one of the three mulches was applied immediately. To prevent smothering, it was necessary to remove part of the heavy hay mulch following germination; otherwise, no attention was given the plots between sowing and the final seedling count 14 weeks later.

The number of seedlings established ranged from 12 to 208 per milacre, with a mean of 57.6 (table II). The heaviest crop of seedlings was obtained under the heavy hay mulches, followed by light hay and pine straw mulch. As there were no unmulched quadrats with which to compare results, it is not possible to say that the successful seedling catch is entirely due to the mulching, but it is a reasonable assumption, judging from the complete failure of the original surface sowing.

*Forest Cover Types.*—All the foregoing tests were conducted on open cut-over land. The question naturally arose as to the protective value of other forest conditions. Nine quadrats of 60 square feet each were therefore sown in each of 4 other conditions: (1) under a dense old-field stand of longleaf pine, (2) in oak brush stands unburned for 4 years, (3) in grassy areas unburned for 1 year, and (4) in grassy areas unburned for 3 years. Seed with wings were dropped in

TABLE II. *Effect of mulch upon survival of longeaf pine seedlings*

| Treatment | Number of quadrats | Mean number of seedlings per milacre | Standard error of mean |
|---|---|---|---|
| Light hay | 60 | 57.5 | ±2.64 |
| Heavy hay | 30 | 117.6 | ±8.03 |
| Total hay | 90 | 77.5 | ±4.37 |
| Pine straw | 135 | 44.3 | ±1.39 |
| Grand total | 225 | 57.6 | ±2.21 |

a manner closely simulating natural seed-fall, and results were recorded in terms of the number of seed reaching mineral soil, the number of seed becoming entangled in the rough or suspended in the leaf litter, and the number of seedlings finally established.

The 1-year rough proved to be only a slight barrier to seed reaching mineral soil, since 46 per cent reached the soil at the time of sowing and much of the remainder reached the soil within 2 weeks. The amount of seed readily reaching the mineral soil on the 3-year rough was 15 per cent; in the oak brush, 6 per cent; and in the old-field stand, 2 per cent. Following sowing there was a marked loss of seed in all cover types except the old-field, but the seed not lost gravitated to the lower layers of debris, especially from the upper portions of rough to the undecomposed organic material on the surface of the soil. This was aided by wind, rain, and the structure of the seed itself; the weight and spiral twist of the wing caused a boring action that helped the seed to work down through the litter to the mineral soil.

Ten weeks after sowing, practically all seed in the grass rough and oak litter that had not been consumed had germinated, while almost one-fourth of the seed sown under the old-field stand was still suspended in the litter. Much of the suspended seed was spoiled and had probably been rejected by predators.

Records of seedling establishment showed that in the 1-year rough only 1 per cent of the total seed sown produced seedlings. The corresponding percentages in the other cover types were: 3-year rough, 1.2 per cent; oak brush, 0.6 per cent; and old-field stand, 14.4 per cent. Not only was the latter percentage conspicuously better than the others, but the distribution of seedlings was exceptionally good; seedlings occurred in all sample quadrats in the old-field type but in only about 10 per cent of the sample quadrats in the other cover types.

The protection provided the seed in this test properly should be broken down into two parts, that provided by the material and condition of the cover, and the biological environment. Bird and rodent populations were distributed fairly regular over the cut-over and scrub oak types. It is a known fact, however, that the birds responsible for the ravages of seed are found in limited numbers and seldom appear in flocks in dense stands of pines such as the old-field stand. Evidently in this case the environmental protection completely eclipsed that provided by the ground cover.

### SEEDBED PREPARATION

The purpose of these studies was to determine the effects of seedbed manipulation upon the germination of longleaf and slash pine seed and upon the survival of the seedlings. Some of the studies were made in the greenhouse, where seed loss could be eliminated and where surface-soil conditions and available water could be controlled; while other studies were conducted in the field under a natural biological environment. These two groups of studies will be discussed separately.

### Greenhouse Studies

*Character of Seedbed Surfaces.*—The first study was made to determine the effects of the character of seedbed surface upon subsequent seed germination and survival. Twelve surface conditions were chosen:

1. Raw subsoil (Norfolk $A_2$ horizon) essentially devoid of organic matter.
2. Mixed soil (Norfolk sand) from the uppermost 3 inches of the soil profile.
3. Surface 3 inches of soil (Norfolk sand) incinerated in a container for ½ hour.
4. Surface soil covered with ½ inch of undecomposed pine needles.
5. Surface soil covered with ½ inch of pine-straw humus.
6. Surface soil covered with ½ inch of pine-straw ash.

7. Surface soil covered with ½ inch of undecomposed oak leaves.
8. Surface soil covered with ½ inch of oak-leaf humus.
9. Surface soil covered with ½ inch of oak-leaf ash.
10. Surface soil covered with ½ inch of undecomposed broom-sedge.
11. Surface soil covered with ½ inch of broom-sedge humus.
12. Surface soil covered with ½ inch of broom-sedge ash.

The three surfaces with no covering (conditions 1–3) and the nine surfaces with three types of covering in three different forms (conditions 4–12) were replicated six times each. Separate analyses were made for germination, penetration, and survival. The three surface conditions consisting of ash were highly alkaline, with a pH of at least 8.21; all the others had a pH of about 5; *i.e.*, they were moderately acid. The tests were conducted in perforated metal flats, in each of which were sown 20 longleaf and 20 slash pine seeds. These were watered daily until germination was complete, after which they were watered at intervals of several days until the end of the test.

The results of this experiment are summarized in table III, in which it is noted that 67.50 to 95.85 per cent of the longleaf pine seed germinated except on surfaces covered with undecomposed pine

needles or broom-sedge. For slash pine the germination was 41.65 to 82.50 per cent, except on four surfaces covered with undecomposed material or partly decomposed pine litter. The poor germination on raw litter was caused largely by mechanical interference; the litter prevented the seed from reaching the moist soil.

For longleaf seed, the undecomposed litter is the only treatment that seems to affect significantly the germination per cent. For slash pine the germination was better on the mineral surfaces, and on the two surfaces covered with decomposed sedge and oak litter, than on other surfaces.

Germination per cent did not show the entire effect of surface cover treatment. In table IV is given the percentage of germinated seed with radicles that penetrated the soil. The best survival for longleaf pine was on the mineral surface. On the surfaces covered with partly decomposed litter, survival was somewhat less; on the ash-covered surfaces, it was considerably less; and on the surface covered with undecomposed litter, it was almost zero. Slash pine survived better than longleaf on most of the surfaces covered with partly decomposed litter or ash; but on the mineral surfaces, longleaf survived a little better than slash.

Longleaf pine seed germinated much more promptly than did slash pine. The

TABLE III. *Germination percentages for different seedbed surfaces*

| Character of seedbed | Longleaf pine | | | | Slash pine | | | | Average |
|---|---|---|---|---|---|---|---|---|---|
| | Pine needles | Sedge | Oak leaves | All types litter | Pine needles | Sedge | Oak leaves | All types litter | |
| Soil covered ½-inch deep with: | | | | | | | | | |
| Undecomposed material. | 2.5 | 20.85 | 67.50 | 30.30 | 5.00 | 1.65 | 3.35 | 3.35 | 16.80 |
| Humus. | 85.85 | 94.15 | 95.85 | 91.95 | 25.00 | 75.00 | 82.50 | 60.85 | 76.40 |
| Ash. | 95.00 | 95.85 | 95.85 | 95.55 | 43.35 | 41.65 | 65.85 | 50.30 | 72.90 |
| Average. | 61.10 | 70.30 | 86.40 | 72.60 | 24.45 | 39.45 | 50.55 | 38.15 | 55.35 |
| Soil uncovered: | | | | | | | | | |
| Raw subsoil. | | | | 85.85 | | | | 78.35 | |
| Topsoil mixed. | | | | 88.35 | | | | 82.50 | |
| Topsoil burned. | | | | 85.00 | | | | 69.15 | |

TABLE IV.    *Percentage of germinated seed that penetrated the soil when seed were sown on various kinds of seedbed surfaces*

| Character of seedbed | Longleaf pine | | | | Slash pine | | | | Average[4] |
|---|---|---|---|---|---|---|---|---|---|
| | Pine needles | Sedge | Oak leaves | All types litter | Pine needles | Sedge | Oak leaves | All types litter | |
| Soil covered ½-inch deep with: | | | | | | | | | |
| Undecomposed material. | .00 | 4.00 | 1.23 | 1.83 | 100.00 | 50.02 | 100.00 | 91.66 | 10.74 |
| Humus.............. | 88.35 | 93.81 | 96.52 | 93.05 | 93.33 | 98.89 | 97.98 | 97.72 | 94.91 |
| Ash................. | 51.75 | 53.04 | 20.87 | 41.86 | 48.08 | 84.00 | 72.15 | 68.51 | 51.05 |
| Average [4]........... | 68.18 | 66.40 | 43.73 | 57.91 | 67.05 | 92.96 | 86.81 | 84.71 | 67.14 |
| Soil uncovered: | | | | | | | | | |
| Raw subsoil.......... | | | | 100.00 | | | | 98.92 | |
| Topsoil mixed........ | | | | 100.00 | | | | 93.94 | |
| Topsoil burned....... | | | | 100.00 | | | | 95.23 | |

rapidity with which it germinated, however, was a disadvantage in the case of the strongly alkaline (ash-covered) surfaces. Under these soil conditions, the radicles failed to enter the soil and grew parallel to the surface for a considerable distance. The alkaline reaction remained high, and plasmolysis of the tender radicles was evident. The high pH value of the surface also induced abnormal loss from fungi. Frequent watering of the soil, however, caused a noticeable leaching of the alkali, so that by the time slash pine seed began to germinate, some 2 to 3 weeks later, the pH value was lower (*i.e.,* the ash was less alkaline), and the radicles had less difficulty in entering the soil. Slash pine also exhibited a greater tolerance to alkaline conditions than did longleaf.

*Soil Compactness and Weight of Seed.* —Another test was conducted for the purpose of studying the effect of the compactness of the soil and of the weight of the seed on the germination and root penetration of longleaf pine. Soil compactness is readily alterable by man and animals, but little is known concerning the resultant effect on longleaf pine seed and seedlings.

The test included three natural soil-texture classes: Norfolk sand surface soil; Norfolk fine sandy-loam surface

soil; and Susquehanna subsoil, a stiff, plastic clay, representative of many eroded areas. Three sample areas were chosen at random within each soil class, and nine samples were taken from each, *i.e.,* a total of 27 samples was taken from each soil class. These samples were then divided into three parts and given the following treatments: (1) sifted and placed back in the flats; (2) retained in normal condition; and (3) compressed within the flats by mechanical force. Longleaf pine seed was divided into three weight classes (61–85, 86–110. and 111–135 milligrams, respectively) and assigned to the flats at random. Thirty seeds were sowed in each flat. The study therefore comprised 3 soil classes, 3 degrees of soil compaction, and 3 weights of seed. Penetrometer[5] tests taken at the outset of the work showed that the three soils could be loosened materially but that mechanical compression did not increase necessarily the compaction of the normal soil. Germination was good on all three classes of soil and was fairly uniform, varying

[4] Computed from the original data and not an average of percentages.

[5] The New York Testing Laboratory penetrometer. This instrument measures the depth to which a standard needle will penetrate during a given time (5 seconds being the standard) per 100 grams of load applied.

from 55.57 per cent to 84.43 per cent. Although the difference is not great, in general the germination was lower for the lightest seed and on the most compacted soils. The percentage of seed that germinated in the 27 treatment classes are listed in table V.

Table VI gives the percentage of mortality among the seed that germinated but that failed to penetrate the soil. From this table it can be seen that the mortality

TABLE V. *Germination percentages for longleaf pine seed on several kinds of soils compacted to various degrees*

| Compaction | Seed weight (grams) | | | |
|---|---|---|---|---|
| | 61–85 | 86–110 | 111–135 | Average |
| *Susquehanna subsoil* | | | | |
| Loose            1 | 68.90 | 80.00 | 73.33 | 74.07 |
| Normal           2 | 66.67 | 71.10 | 84.43 | 74.07 |
| Mechanically   3 compacted | 62.23 | 80.00 | 61.10 | 67.77 |
| Average | 65.93 | 77.03 | 72.97 | 71.97 |
| *Norfolk fine sandy-loam surface soil* | | | | |
| Loose            1 | 72.23 | 72.23 | 80.00 | 74.80 |
| Normal           2 | 60.00 | 81.10 | 75.57 | 72.23 |
| Mechanically   3 compacted | 63.33 | 55.57 | 58.90 | 59.27 |
| Average | 65.20 | 69.63 | 71.47 | 68.77 |
| *Norfolk sand surface soil* | | | | |
| Loose            1 | 66.67 | 78.90 | 71.10 | 72.23 |
| Normal           2 | 68.90 | 81.10 | 84.43 | 78.13 |
| Mechanically   3 compacted | 70.00 | 72.23 | 81.10 | 74.43 |
| Average | 68.53 | 77.40 | 78.90 | 74.93 |
| *All soils* | | | | |
| Loose            1 | 69.27 | 77.03 | 74.80 | 73.70 |
| Normal           2 | 65.20 | 77.77 | 81.47 | 74.80 |
| Mechanically   3 compacted | 65.20 | 69.27 | 67.03 | 67.17 |
| Average | 66.53 | 74.70 | 74.43 | 71.90 |

TABLE VI. *The mortality per cent of longleaf pine seedlings under conditions of three degrees of soil compaction and soil types between the time of germination and root penetration*

| Compaction | Seed weight (grams) | | | |
|---|---|---|---|---|
| | 61–85 | 86–110 | 111–135 | Average |
| *Susquehanna subsoil* | | | | |
| Loose            1 | 27.43 | 30.54 | 36.36 | 31.50 |
| Normal           2 | 76.65 | 90.62 | 73.71 | 80.02 |
| Mechanically   3 compacted | 98.18 | 97.21 | 100.00 | 98.38 |
| Average | 66.28 | 72.13 | 68.52 | 69.15 |
| *Norfolk fine sandy-loam surface soil* | | | | |
| Loose            1 | 30.78 | 24.60 | 36.12 | 30.70 |
| Normal           2 | 37.06 | 36.99 | 38.24 | 37.43 |
| Mechanically   3 compacted | 26.32 | 34.00 | 49.07 | 36.22 |
| Average | 31.24 | 31.93 | 40.44 | 34.66 |
| *Norfolk sand surface soil* | | | | |
| Loose            1 | 31.65 | 26.74 | 37.51 | 31.80 |
| Normal           2 | 30.62 | 17.80 | 39.48 | 29.39 |
| Mechanically   3 compacted | 28.57 | 33.83 | 43.86 | 35.83 |
| Average | 30.25 | 25.84 | 40.39 | 32.30 |
| *All soils* | | | | |
| Loose            1 | 29.93 | 27.39 | 36.63 | 31.34 |
| Normal           2 | 48.26 | 46.68 | 50.90 | 48.71 |
| Mechanically   3 compacted | 50.00 | 58.28 | 62.46 | 56.97 |
| Average | 42.48 | 43.64 | 49.57 | 45.34 |

was highest on the normal and compact Susquehanna subsoil. Loosening, however, caused no appreciable reduction of mortality on the Norfolk soils.

The heaviest seed, despite its better germination, developed radicles that did not penetrate as well as those of lighter seed. Once the seedling radicles penetrated the soil, however, survival appeared to be assured; none of the factors (seed

TABLE VII. *Mortality per cent of all longleaf seedlings that failed to establish themselves after germination*

| Compaction | | Seed weight (grams) | | | |
|---|---|---|---|---|---|
| | | 61–85 | 86–110 | 111–135 | Average |
| *Susquehanna subsoil* | | | | | |
| Loose | 1 | 32.25 | 37.50 | 37.88 | 36.00 |
| Normal | 2 | 86.67 | 95.33 | 81.59 | 87.51 |
| Mechanically compacted | 3 | 98.20 | 98.61 | 100.00 | 98.92 |
| Average | | 71.34 | 76.45 | 72.08 | 73.42 |
| *Norfolk fine sandy-loam surface soil* | | | | | |
| Loose | 1 | 53.84 | 35.38 | 40.28 | 43.08 |
| Normal | 2 | 38.89 | 42.47 | 44.11 | 42.04 |
| Mechanically compacted | 3 | 28.07 | 34.00 | 50.93 | 37.50 |
| Average | | 40.90 | 37.76 | 44.57 | 41.11 |
| *Norfolk sand surface soil* | | | | | |
| Loose | 1 | 41.67 | 28.17 | 40.63 | 36.40 |
| Normal | 2 | 46.77 | 23.29 | 40.79 | 36.50 |
| Mechanically compacted | 3 | 31.75 | 35.38 | 67.13 | 45.78 |
| Average | | 39.99 | 28.71 | 49.76 | 39.54 |
| *All soils* | | | | | |
| Loose | 1 | 42.78 | 33.66 | 39.61 | 38.53 |
| Normal | 2 | 57.94 | 51.91 | 55.92 | 55.13 |
| Mechanically compacted | 3 | 51.69 | 59.35 | 72.38 | 61.21 |
| Average | | 50.66 | 47.93 | 55.40 | 51.34 |

weight, soil class, or degree of compaction) caused any significant loss of seedlings during the first 3 months after germination.

Actual survival of seedlings, that is, ability to penetrate and establish themselves, is the ultimate test of a seedbed. Fewer seedlings were produced on the Susquehanna subsoil than on the surface soils from the Norfolk group (Table VII). Loosening heavy soils increased

the total number of seedlings, but mechanical compaction had no significant effect on any of the soils insofar as laboratory germination and survival were concerned. Seed weight, on the whole, proved not to be significant, although for certain soils responses were noted. Seed of medium weight did poorly on the Susquehanna subsoil and well on Norfolk sand, where heavy seed made a poor showing. Seedling radicles also increased in total length as a result of their continued growth while attempting to enter the hard surface on which the seed was sown.

Also the length of time necessary for the seed to germinate was unaffected by the compaction of the soil. Loosening, however, shortened the period of penetration by more than a day; this is important when the difference may mean establishment or desiccation (Table VIII).

TABLE VIII. *Elapsed time for germination and penetration*

| Period of examination | Mean length of period in days | | |
|---|---|---|---|
| | Compacted soil | Normal soil | Loosened soil |
| Germination period... | 19.64 | 20.03 | 21.98 |
| Period to penetrate soil............. | 8.01 | 9.21 | 6.84 |
| Total elapsed time.... | 27.65 | 29.24 | 28.82 |

*Water Relations.*—In the studies described above, the volume of water used was held constant at a predetermined amount, assumed to be satisfactory. To determine how much water was necessary to bring about germination, the optimum amount, and the most effective distribution, an experiment consisting of nine degrees of watering, each replicated three times, was established according to the schedule shown in table IX.

Free-draining containers filled with air-dry well-mixed Ruston sandy-loam top

TABLE IX.  *Schedule of watering test*

| Amount of water expressed in inches of rainfall | Number of times applied | Time of application |
|---|---|---|
| 0.1 | 36 | Each of 36 days |
| 0.2 | 18 | Every other day |
| 0.3 | 12 | Every 3rd day |
| 0.4 | 9 | Every 4th day |
| 0.6 | 6 | Every 6th day |
| 0.9 | 4 | Every 9th day |
| 1.2 | 3 | Every 12th day |
| 1.8 | 2 | Every 18th day |
| 3.6 | 1 | First day only |

soil were used as flats; 20 longleaf pine seeds were sown on the surface of each flat; and water was applied on the date of sowing and thereafter according to schedule. Germination and root penetration records were made at 1- or 2-day intervals for 36 days, when the test was completed.

At the end of the 36-day period, it was found that the final germination percentages were substantially the same regardless of watering treatment. The promptness of germination, however, was very different for different frequencies and amounts of watering. Those seed which received more than 1 inch of water at the start germinated 80 to 100 per cent before the second watering, or 70 to 87 per cent within 10 days. The seed that received from 0.1 to 0.3 inch of water at each watering were intermediate in response and germinated 48 to 76 per cent within 10 days, while those that received 0.4 to 0.9 inch of water germinated only 20 to 38 per cent in 10 days. The curves for each of the three groups are given in figure 1. The heavily watered group also showed root penetration within 14 days, considerably sooner than those on other watering schedules. A comparison of the effect of season was made by repeating the original December test in the following March. The total germination in the spring was much poorer than in the winter, but the relative effects of different watering treatments were substantially the same.

## Field Studies

*Seedbed Conditions.*—Simultaneously with the greenhouse studies, a seedbed study was made in the field. A series of seedbeds was arranged around each of 24 seed-bearing longleaf pines (separated by at least 250 yards from any other seed tree) in such a way that 3 seedbed treatments, 4 directions, and 3 distances from the seed source could be studied. The seedbed treatments consisted of (1) broadcast burning, (2) cultivation (spading), and (3) undisturbed, 3-year grass rough. The directions considered were northeast, southeast, southwest, and northwest, and the distances were 0–30 feet, 30–47 feet, and 47–64.5 feet, respectively, from the seed trees. The experiment was established 2 months prior to seedfall in 1935, a year when there was an excellent seed crop. Seedling counts were made in February 1936, May 1936, and May 1937 (Table X).

The first count showed that 53 per cent of all the seedlings occurred in the rough, 30 per cent were in the cultivated areas, and only 17 per cent were on the burned quadrats. Distribution of seedlings around the tree was also significant; the areas south of the trees contained 57 per cent of the seedlings.

The occurrence of prevailing north, northeast, and northwest winds during the period of seedfall readily explains the presence of more seedlings to the south than to the north. Inasmuch as the less frequent southeast and east winds are also likely to be accompanied by greater moisture, which retards seed dispersal, it is surprising that so many seedlings were found on the north side of the trees.

Within the relatively narrow zone of measurement, distance from the tree was not significant. Judging from a few seedling counts made at 65 to 100 feet from the seed trees, detailed counts should have been made for at least 130 feet from the trees.
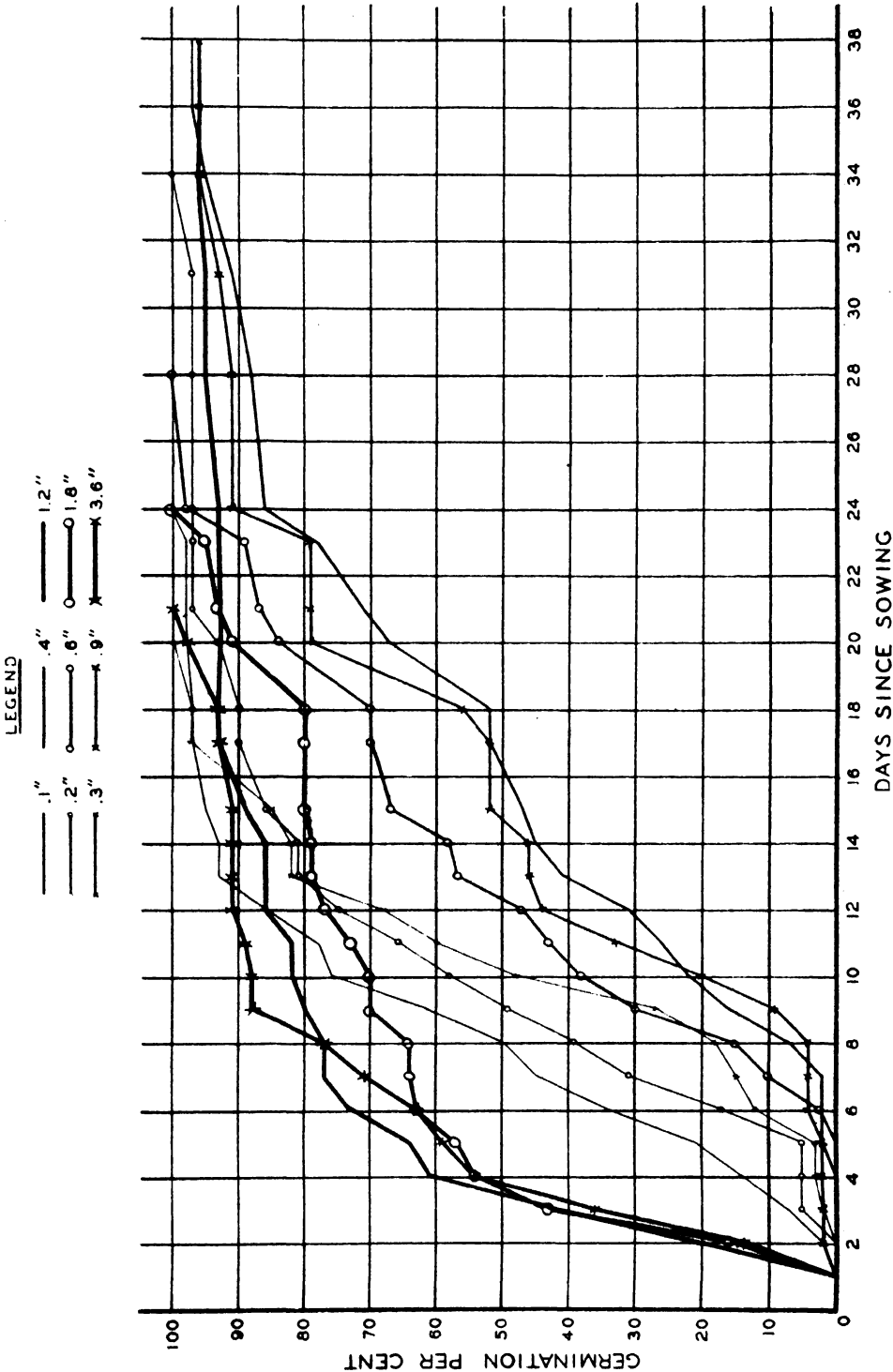
FIG. 1.   The effect of varying the frequency and amount of water drainage during the germination period of longleaf pine seed.

TABLE X. *Average number of seedlings per milacre at time of first count (February 1936) and percentage that survived during the following 3 and 15 months, respectively*

| Quadrant | Treatment | Distances from seed trees | | | | | | | | | | |
| | | 0 to 30 feet | | | 30 to 47 feet | | | 47 to 64.5 feet | | | Mean | | |
| | | Initial catch of seedlings | Per cent survival | | Initial catch of seedlings | Per cent survival | | Initial catch of seedlings | Per cent survival | | Initial catch of seedlings | Per cent survival | |
| | | | May 1936 | May 1937 | | May 1936 | May 1937 | | May 1936 | May 1937 | | May 1936 | May 1937 |
| Northeast | Cultivated | 11.0 | 82 | 41 | 11.7 | 71 | 46 | 11.6 | 59 | 41 | 11.4 | 70 | 42 |
| | Rough | 26.0 | 75 | 60 | 21.0 | 83 | 75 | 24.6 | 87 | 59 | 23.9 | 81 | 52 |
| | Burned | 11.0 | 86 | 36 | 4.3 | 54 | 38 | 6.4 | 75 | 59 | 7.2 | 77 | 44 |
| Southeast | Cultivated | 17.0 | 82 | 65 | 12.0 | 81 | 56 | 19.4 | 77 | 57 | 16.1 | 80 | 59 |
| | Rough | 30.5 | 84 | 66 | 29.7 | 84 | 48 | 27.0 | 87 | 61 | 29.1 | 84 | 58 |
| | Burned | 10.0 | 80 | 30 | 10.7 | 72 | 47 | 9.8 | 90 | 61 | 10.2 | 80 | 46 |
| Southwest | Cultivated | 19.0 | 76 | 47 | 21.0 | 84 | 57 | 18.8 | 78 | 52 | 19.6 | 80 | 54 |
| | Rough | 26.5 | 81 | 34 | 30.7 | 89 | 45 | 26.6 | 84 | 50 | 27.9 | 85 | 43 |
| | Burned | 14.5 | 79 | 55 | 7.7 | 78 | 61 | 5.0 | 80 | 32 | 9.1 | 79 | 52 |
| Northwest | Cultivated | 9.0 | 83 | 61 | 11.0 | 82 | 58 | 15.2 | 78 | 41 | 11.7 | 80 | 51 |
| | Rough | 20.0 | 88 | 75 | 27.0 | 91 | 72 | 22.2 | 83 | 60 | 23.1 | 88 | 69 |
| | Burned | 10.5 | 76 | 62 | 6.3 | 84 | 63 | 4.6 | 78 | 43 | 7.1 | 80 | 58 |
| Average | Cultivated | 14.0 | 81 | 53 | 13.9 | 79 | 54 | 16.1 | 73 | 48 | 14.7 | 78 | 52 |
| | Rough | 25.6 | 82 | 59 | 27.1 | 87 | 60 | 25.1 | 85 | 58 | 25.9 | 85 | 58 |
| | Burned | 11.5 | 80 | 46 | 7.2 | 72 | 52 | 6.4 | 81 | 49 | 8.4 | 79 | 50 |

Wide variations were obtained from losses of seedlings in the zones nearest the tree to tree which could not be attributed to tree height, to cone crop, or to other measured factors. The first differences were substantially maintained during the 15 months following germination, as shown by the second and third examinations. The average per-acre stand was 2080 seedlings on the burned quadrats, 3500 on the cultivated, and 7500 in the rough.

The mortality rate, which declined noticeably during the last 12 months, showed a trend that, if continued, would have insured sufficient seedlings for ample stocking on any of the seedbeds; but the burned seedbed with its lower stocking and slightly higher mortality, was in a more critical condition than any of the others. Root competition between newly established seedlings and isolated seed trees was not emphasized by any abnormal seed trees. As the study terminated at this point, it is impossible to state what might have been the final results in terms of seedlings that actually started height growth.

DISCUSSION

The importance of protection of long-leaf pine seed from birds and rodents is shown by the foregoing tests. The birds chiefly responsible for the loss of seed were several species of blackbirds, the mourning dove, the southern meadowlark, and the quail (Burleigh, '38). Although mice and squirrels caused some losses of seed, they were of secondary importance. Birds, however, must be considered as primary destructive agents; being highly mobile there is every reason to believe that they migrate in large flocks to the locality in which food is available, wipe

out the seed crop within a few days, and fly on to other supplies. Such was apparently the case in the winter of 1935–1936, when a good seed crop of somewhat restricted extent in south Mississippi attracted a large number of migratory birds.

Another interesting point was the close association between the food habits of the depredators and the temperature conditions. Through November 1935, for example, the temperature remained high, insect life was abundant, and although pine seed was being dispersed, little of it was eaten. In early December, however, when a period of sharp frosts occurred, and insect life became scarce, the destruction of seed was immediately evident. Also those seed which had germinated were clipped or pulled from the partially established seedlings, with the result that a large part of the seed crop was destroyed within a week.

Practical methods of seed protection must be divided into two groups: those applicable to direct-seeding methods, and those to be used with natural reproduction. Of the direct-seeding methods tested, the wire-screen tube seems most promising. It affords high protection and is effective throughout the entire sowing period (October to March). The less satisfactory results obtained with these tubes on cultivated soils and burned surfaces probably were due to faulty sowing technique. Making the tubes cost about $2.25 per thousand, while installing them and sowing the seed cost $2.00. The use of small machines for manufacture, and improved field sowing, would reduce these costs materially.

Drill sowing gave results promising enough to justify further investigation. Success along this line of approach, however, depends largely upon an improved design of drill; present hand-drill machines are not designed for the rough work demanded of them. A combination of mobility, flexibility, and strength not found in the ordinary hand seeder is needed.

Mulches are useful in providing partial protection against the ravages of birds, but may be positively detrimental where there are many rodents, which are likely to seek both protection and food under the mulch.

Protecting seed sown under natural conditions is an even more difficult task than protecting those directly seeded, but the results obtained by sowing under the old-field stand should not be overlooked. While this stand was only of pulpwood size and under normal conditions would not be harvested for several years, the results indicate that a heavy overstory of mature pine timber might be especially helpful in providing protection for naturally sown seed. If a mature stand provided the same protective cover as the second-growth timber did, every effort should be made to obtain a good "catch" of seedlings in advance of logging, while the timber still affords such cover.

Another important problem is how to get the most from the seed present. The watering test indicates that a few heavy rains immediately following the fall of longleaf seed would stimulate germination and early establishment, thereby reducing the period during which there is the danger of destruction by birds and rodents. It is easier, however, to improve ground cover and soil conditions, and the results of these studies show the possibilities in that direction. Mineral soils proved to be an excellent bed for pine seed, but of particular interest was the poor response obtained from seed sown on surfaces covered with leaf ash. This confirms the opinion of Jamwal ('39) who attributed to poor germination the failure to establish seedlings. Our results indicated that poor establishment resulted not from inability of the seed to germinate but from the inability of the radicles to penetrate the ash-covered soil. Apparently some physiological response in the radicles prevented their passage into the soil. It might be concluded that burning of very heavy roughs at the beginning of the period of seedfall would

be undesirable, since the resulting mantle of ash might prevent the seedlings from becoming established. Such conditions would obtain especially in years when rainfall is slight during the period of germination. No field tests, however, have been made to substantiate these deductions.

The effects of soil tillage upon the establishment of seedlings were much less striking than anticipated except possibly on the very dense subsoil. Where Susquehanna subsoil is exposed by erosion, the chances of reproducing the area to pine are very poor, since here the seed are exposed and the establishment of the seedlings is retarded owing to the unfavorable physical nature of the soil. On this or similar soil, cultivation prior to a seed crop would greatly enhance the probability of reestablishment of a pine stand. Compaction, such as results from concentrated grazing, would not be detrimental, provided trampling was discontinued at the time of seedfall.

It is not surprising, therefore, that the field test of seedbeds failed to conform entirely with the results obtained in the greenhouse. The fact that the number of seedlings secured on the 3-year rough greatly exceeded that obtained on surface-burned or cultivated plots, clearly demonstrated the relative importance of seed protection and seedbed preparation.

Without seed protection, the added benefits of exposure of mineral soil, cultivation (in the case of dense soils), and even favorable rainfall are all of secondary importance. The primary problem, consequently, is to provide the best seedbed commensurate with maximum seed protection.

## SUMMARY

Field tests show that longleaf pine seed must be protected from birds and (to a less extent) from rodents, if a stand of seedlings is to be established. In artificial reforestation, the use of small wire tubes, mulches, and the mechanical drill seeder gave promising results. A test of the protective value of cover type indicated that a heavy stand of second-growth old-field pine was much more effective than grasslands or scrub oak stands.

Greenhouse tests showed that longleaf seed germinated and became established best on mineral soils and on light, well-watered humus. Heavy deposits of ash from recently burned litter were very detrimental to the establishment of longleaf seedlings. The physical condition of the surface soil was also important; while the hardness or compaction of the soil did not lower materially the germination of pine seed, it affected noticeably the penetration of the soil by the radicles. Mechanical loosening of dense soils favored decidedly the establishment of the seedlings. The rate of germination of longleaf seed varied with the quantity of water applied and the frequency of application. Also one or two soakings at long intervals hastened germination.

In a field trial made for the purpose of testing the information obtained from the direct-seeding work and the greenhouse trials, the "catch" from natural seedfall on burned and cultivated seedbeds was poorer than on the natural rough. It was apparent that the protective value of the rough was more important than the favorable soil conditions supplied by burning or cultivating. If adequate protection can be secured for longleaf seed, and if the factors which proved so advantageous in the greenhouse can be applied in the field, a distinct increase in number of seedlings from a given seed crop should result.

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# CERTAIN ECOLOGICAL CHARACTERISTICS OF ORANGE SNEEZEWEED

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## INTRODUCTION

Orange sneezeweed (*Helenium hoopesii* A. Gray), a stout perennial herb of the composite family, has become one of the most important poisonous plants (Marsh, et al, '21, and Dayton, et al, '37) on the summer range lands in the central Rocky Mountains. This plant is distributed from eastern Oregon to western Montana and southward to New Mexico and California, attaining its maximum economic importance in Colorado and Utah where heavy losses of sheep occur frequently on areas supporting dense stands. In recent years this species has apparently spread over large areas heretofore uninfested, and in many localities sparse stands have become noticeably denser. In fact, the extended distribution of the plant and its marked increase in frequency is seriously handicapping profitable sheep grazing in some localities.

Because of the growing importance of orange sneezeweed, the Rocky Mountain Forest and Range Experiment Station began in 1938 to investigate its characteristics and the ranges on which it occurs. Thus far, 37 different areas in the mountains of western Colorado, where the plant is particularly dense, have been studied. A series of 10 circular, equally spaced, 100 square-foot plots were studied on each area by the square-foot density method (Stewart and Hutchings, '36). In addition to this survey of density and relative composition of vegetation, special notes and measures were recorded in order to ascertain the external nature of the habitat; the abundance, growth habits, and plant associates of orange sneezeweed; and the condition of the range in relation to grazing. With special reference to the mountains of western Colorado, these studies have disclosed certain growth characteristics that are described in this discussion.

## GENERAL DESCRIPTION

Orange sneezeweed is usually found in patches of varying density and size, but may occur as scattered individuals. Most mature plants consist of one to several flowering stems and a larger number of rosettes, all closely massed into a clump 4 to 12 inches across. The flowering stems average about two feet in height, but may range from one to four feet tall. The stem is leafy and bears an average of four flower heads which are two to three inches broad. The ray flowers are orange yellow; the disk flowers brownish orange and both kinds are fertile. The leaves are generally large, entire, deep green, glandular-dotted, parallel-veined, oblong-lanceolate and sessile; the lower leaves are spatulate with a long-tapering base. The plants have a short woody taproot from which new rosettes arise.

Orange sneezeweed makes its optimum growth (up to 39 per cent of the plant cover) between 9,000 and 10,000 feet elevation on good, loamy well-drained soils of level or gently sloping areas in parks or dry meadows of the aspen (*Populus tremuloides aurea*) and hoary sagebrush (*Artemisia cana*) types, or openings in the Engelmann spruce (*Picea engelmanii*) type. The treeless areas and dry meadows invariably support the densest stands of sneezeweed.

## PLANT ASSOCIATES

The plant species most frequently associated with orange sneezeweed from the standpoint of frequency of association

FIG. 1. The development of offshoots on root crowns of orange sneezeweed on Sept. 25, 1938. Each specimen is the lower part of a decadent flower stalk. The new growth cycle starts as the old one ends.

and density are, in approximate order: western yarrow (*Achillea lanulosa*), dandelion (*Leontodon taraxacum*), slender wheatgrass (*Agropyron pauciflorum*), strawberry (*Fragaria glauca*), cinquefoil (*Potentilla filipes*), peavines (*Lathyrus* spp.), Letterman needlegrass (*Stipa lettermani*), Richardson geranium (*Geranium richardsonii*), lupines (*Lupinus* spp.), wild-daisy (*Erigeron* sp.), and trisetum (*Trisetum spicatum*).

## NATURAL ENEMIES

Many sneezeweed plants were infested with a rust, *Puccinia conspicua*. The alternate host of the rust is junegrass (*Koeleria cristata*). Two kinds of insect larvae were found living on sneezeweed. One kind inhabits the receptacle, and evidently causes considerable damage to the developing fruits by hollowing out the receptacle. A different kind of larva inhabits and devours large portions of the thickened taproot. Mature stages of these insects have not been found, but both kinds belong to the Lepidoptera and the root larva to the family Olethreutidae.

## REPRODUCTION, MIGRATION AND ESTABLISHMENT

Orange sneezeweed reproduces by seed and by offshoots arising as adventitious

buds from the taproots (fig. 1). Migration is chiefly by seeds, but once established the stands are maintained largely by offshoots.

In 1938, the plants were in full bloom about August 1, the fruit matured late in August, dissemination began about September 1, and the flower stalks were dead by September 20.

As the growth cycle reached its climax, that is, in the latter part of August when the fruits were maturing, adventitious buds were formed on the short woody taproots. These buds developed into offshoots or new rosettes. The first buds were noticed on August 29, but since some buds had already grown into young shoots about one inch long, the first buds probably developed as early as August 22. On September 22, 36 plants that flowered in 1938 and an equal number that did not flower were collected randomly for counts and measures of buds and new shoots. A summary of these data (Table I) shows that the 36 flowering plants produced 216 buds and new plants or an average of six per plant, as compared with a total of 18 or an average of 0.5 per plant for the 36 nonflowering plants. The new plants ranged in size from small buds to rosettes five inches in length.

Inspection of offshoots on October 10,

TABLE I. *The number of buds and young shoots on 36 flowering and 36 nonflowering plants. September 22, 1938*

| | Buds | Shoots by size classes [3] in inches | | | | | Total |
|---|---|---|---|---|---|---|---|
| | | 0–1 | 1–2 | 2–3 | 3–4 | 4–5 | |
| On 36 plants that flowered in 1938 | | | | | | | |
| Total number | 57 | 42 | 49 | 36 | 16 | 16 | 216 |
| Average per plant | 1.6 | 1.2 | 1.4 | 1.0 | 0.4 | 0.4 | 6.0 |
| Per cent | 26.4 | 19.4 | 22.7 | 16.7 | 7.4 | 7.4 | 100 |
| On 36 plants that did not flower | | | | | | | |
| Total number | 10 | 1 | 0 | 4 | 3 | 0 | 18 |
| Average per plant | 0.3 | 0.0 | 0 | 0.1 | 0.1 | 0 | 0.5 |
| Per cent | 56.6 | 5.6 | 0 | 22.2 | 16.6 | 0 | 100 |

[3] Size classes were based on maximum leaf length.

after the first autumn frosts, revealed that the new rosettes were still alive and green, and had attained a height of about 6 inches. Heavy snows at high altitudes prevented further observation of offshoot growth in their native habitat. However, in order to observe the plants during winter, a few mature specimens with offshoots were transplanted to a lower elevation (5000 feet) in late September. One-half of the transplants were covered about 4 inches with a mulch to protect them from low air temperatures. Growth of the offshoots continued for about three weeks after being transplanted. On November 10, most of the offshoots were still green but growth had ceased. The plants under the mulch had made more growth than the exposed plants. Prior to this examination, freezing temperatures had occurred for approximately three weeks, the minimum temperature during the period being 10.4° F. No snow had accumulated to protect the exposed plants.

By January 17, 1939, all exposed leaves had been killed but those covered with a mulch were still green, and one plant that had been covered with snow was also green. The protected plants were still green on January 31, although the soil around them was frozen. Minimum air temperatures were generally below freezing during the period of these observations and on one occasion reached 8.9° F. below zero. The significance of this point is that orange sneezeweed plants remained green until mid-winter when protected by a thin mulch even though the soil in which they grew was frozen. These observations indicate that many orange sneezeweed plants probably remain green under snow in their natural habitat throughout the winter and thereby may start growth ahead of associated herbs in the spring. This feature will be investigated further.

Observations concerning the production of offshoots by orange sneezeweed may be summarized as follows: (1) Generally speaking, offshoots were formed only on the roots of plants that flowered cur-

rently; (2) the offshoots started from adventitious buds that were formed as the upper parts of the flowering stem were dying; (3) growth of the new rosettes continued after other herbaceous plants were killed by frost; (4) it appears probable that the leaves of many orange sneezeweed plants remain green beneath the snow during the winter.

## POISONOUS QUALITIES

The growth habits of orange sneezeweed are largely responsible for its importance as a poisonous plant. Being green earlier in the spring and later in the fall than associated herbaceous plants makes the plant particularly conspicuous. Sheep graze it heavily under these conditions. Further, orange sneezeweed is so hardy and aggressive that it is rapidly dominating areas infested at present and is constantly invading new areas. Because of its vigor and strong vegetative habits, control or eradication is very difficult and expensive. Further ecological studies, combined with eradication tests, may reveal a practical method of controlling orange sneezeweed, but it is of immediate importance to the livestock industry that management practices that will minimize losses be developed for ranges infested with the plant.

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# REVIEWS

## Quantitative Zoology [1]

The modern ecologist is always alert for something new, something really worthwhile, in the field of biometrics. As ecology becomes more and more a quantitative discipline, so must the ecologist master the mechanics and meaning of appropriate statistical methods. One reason this mastery is difficult lies in the fact that many expositions of statistics are prolix, overly technical (for the biologist!) and poorly written. This is somewhat analogous to the situation in elementary zoology where texts dealing with that field are manufactured along mass production scales to the cheerful neglect of scholarship.

What is the answer to this dilemma? A partial answer lies in the writing of books by authors with facility and judgment in both statistics and biology. Biologists are not overly concerned with statistical research; they wish information, known to be sound through routine use, that can be applied to their specific problems. The present book by Simpson and Roe is a volume of this calibre. The authors show great skill in developing those statistical treatments of patent value for run-of-mine biological research. In addition, the book is not merely an expert summary of techniques and examples. It is, rather, a careful and lucid account of the theories and concepts underlying these techniques with a constant drive towards interpreting all results in the light of biological material.

The book starts with a general discussion of the properties of numerical data and mensuration. This is followed by a consideration of frequency distributions from both the empirical and the theoretical point of view. The measurement of central tendency and dispersion follows

on this background. Such parameters as the mean, median, mode, standard, mean and quartile deviations and coefficient of variability are developed critically. The chapters on the normal curve, probability, sampling and comparison of samples are excellent. The reader is able to follow the discussions and see the justification of statistical methods even if he is a complete novice in the field. In Chapter X (Comparison of Samples) the authors point out that the formula for the standard error of a difference between two uncorrelated means

$$\sigma d = \sqrt{\sigma^2_{M_1} + \sigma^2_{M_2}}$$

that is nearly always presented in statistical texts may not have as much reliability for zoological data as the rarely discussed formula

$$\sigma d = \sqrt{\frac{N_1}{N_2} \sigma^2_{M_1} + \frac{N_2}{N_1} \sigma^2_{M_2}}.$$

The discussion of small samples is brief but adequate and includes a useful review of the so-called "Student's Method" and an easily read table of $t$ for estimating probabilities of differences. There is also a unique discussion of statistics as applied to single specimens. This should be useful for individuals working along morphological and taxonomic lines. The treatment of correlation and regression is quite conventional with Fisher's $Z$ favored as a criterion of correlation over the usual $r$. There is a good discussion of $\chi^2$ and contingency and an interesting chapter on growth. The book has an appendix of formulae, a brief bibliography, an index and is of pleasing format. There is no consideration of the analysis of variance other than defining variance as $\sigma^2$. This may be considered a drawback by ecological readers. The experimentalists will be surprised probably at the authors' feeling that coefficients of

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[1] Book review: Simpson, G. G., and Anne Roe. 1939. Quantitative Zoology. *McGraw-Hill Book Co., New York and London.* xvii + 414 pp. 52 figs. $4.00.

variability above 10 per cent are unusual in zoology. However, in the balanced judgment of the reviewer, "Quantitative Zoology" is one of the most useful texts on biometry to appear for some time. It

warrants the close attention of the ecologist.

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## CONSERVATION [1]

This is the second recent text on conservation. The first was Parkins' and Whitaker's "Our Natural Resources and Their Conservation." A third is reported to be in the offing.

Like its predecessor, the present volume consists of a series of sections, each by a different author, and each treating of a group of resources: soil and water, forests, parks and ranges, wildlife, minerals.

No one seems yet to have questioned the sufficiency of this "compartmental" scheme for describing the behavior of land under human use. I do. It is too much like describing the "separate" organs of an animal or plant, and then leaving to inference their collective behavior as an organism.

The compartmental text has advantages for the publisher: it parallels the distribution of expertness among authors, and thus favors the quick production of a factually competent job. But it also parallels the bureaus, sciences, and pressure groups whose propaganda has flooded the student from birth, and whose prevailing vice is intellectual isolation. What the student (and teacher!) now needs is a text which cuts at right angles to these arbitrary divisions of the land problem; a text which describes the common mechanism of soils, waters, plants and animals as one integral whole; a text which treats of farms, forests, ranges and parks not as different resources, but as different uses of a single resource, the properties of which are first described as a single sys-

tem, and then traced in their various land-use manifestations.

As an example of what the compartmental text fails to cover, consider the plant and animal succession. This common denominator of all land problems receives, in this book, thirteen lines of space. Nowhere is it adduced as a universal property of all plant and animal communities. May we assume that the student is familiar with it by reason of his courses in zoology and botany? I think not.

Another example: Soil fertility is described (with admirable force) as the basic concern of agriculture. But what of wildlife, forests, and ranges? The reader might well infer that these can grow on any soil.

Another example: The "balance of nature" gets a sketchy two pages in, the chapter on "other useful wildlife." One might almost infer that balance is the function of hawks and owls! That crops, forests, waters, and soils are part of the balance is left largely to inference.

As a compartmental text, the present volume is a good job. The materials are more explicit and better selected than in any like volume. Their presentation, however, is spotty. Some spots are dulled by that peculiar circumlocution characteristic of government bulletins; others are models of directness and simplicity. Here and there one encounters flashes of real dramatic color, notably in Gustafson's concluding chapters on soil. In Hamilton's chapter on fisheries one can almost taste the salt.

In their judgments of policies and programs, the authors are fair and unusually forthright. None of them, for example,

[1] Gustafson, A. F., H. Ries, C. H. Guise, and W. J. Hamilton, Jr. 1939. Conservation in the United States. *Comstock Publ. Co., Ithaca, N. Y.* 445 pp.

"glosses over" the prevailing failure of private landowners to practice conservation. Some of them soft-pedal the collisions between conflicting interests, such as mosquito-control versus wildlife, power dams versus fisheries. There is no explicit admonition to the student that he, as a citizen, is the ultimate arbiter of these conflicts; that until he develops a critical attitude toward them, many a "conservation" enterprise merely cancels another bearing the same label.

Guise's section on forests includes a new resource category, "wildflowers and other non-commercial plants." Such explicit recognition for this bureauless, lobbyless waif as a legitimate member of the conservation family is encouraging, but one could wish for a less apologetic tone in presenting him to polite society.

The format of the book is good; the photographs abundant and excellent. Each chapter ends with a list of quiz questions, many of which are vague and seem to call for memorization rather than de-

duction. These quiz questions, it seems to me, could have been used to encourage the student to think out his own local applications of the generalized textual material.

The book ends with a fair index, and with lists of titles for supplementary reading. These reading lists omit the authors who, to my mind, have most successfully portrayed land conservation as one integral whole, namely George P. Marsh and Paul B. Sears. The lists contain few ecological titles, but such omission is readily excusable, for few American ecologists have written in terms comprehensible to non-specialized students.

Taking everything together, this book has the faults of its generation, and a good many virtues of its own. It is a step upward toward that common goal: better teaching materials for conservation courses.

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## A HANDBOOK OF THE COMMON INVERTEBRATES OF THE PACIFIC COAST [1]

The area that lies between the upper and the lower limits of the tide on a rocky ocean shore is one of the most densely populated of all life zones. And its animal inhabitants, many of them bizarre in shape and brilliant in color, have a fascination not only for the professional biologist but also for any intelligent observer at the seashore. The monographs and systematic keys prepared by specialists are not readily accessible to laymen, the beginning class in zoology, or the amateur naturalist. To meet the needs of such people, Ricketts and Calvin have prepared a handbook which gives an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific

[1] Ricketts, E. F., and J. Calvin. 1939. Between Pacific Tides. *Stanford Univ. Press,* *Stanford, Calif.* 320 pp., 112 figs., 46 pls. $6.00.

Coast between Sitka, Alaska, and northern Mexico.

To make it possible for a person with little or no biological training to use such a book, the authors have employed an ecological rather than the usual phylogenetic organization. Animals are classified according to their most characteristic habitat and in the order of their commonness, conspicuousness, and interest. The habitat classification is based upon three main factors: (1) degree of wave shock (protected outer coast, open coast, bay and estuary, and wharf piling), (2) type of bottom (rocky shores, sandy beaches, and mud flats), (3) tidal exposure (uppermost, high tide, mid-tide, and low tide horizons).

There is little or no morphological description of the animals and identification must be made chiefly on the basis of

habitat and reference to the line drawings and photographs, almost all of which were made especially for this book. The reproduction of the photographs is above average for books of this kind, but in many cases it does not do justice to the originals, many of which were really superb.

The account of any particular animal may include such items as range, feeding and breeding habits, life history, type of respiration, locomotion, special structures such as pedicellariae, special habits like autotomy or evisceration, and economic use. There are discussions of the adaptations of individuals and communities to the different types of habitat. And there are references to experimental studies on the physiology and behavior of marine invertebrates. The style is clear and interesting, though it frequently lapses into statements that may irritate the biologist and mislead the untrained reader. For example, on page 59, we read, "Sometime in the past few thousand years *Syndesmis* presumably discovered that food-getting conditions on the inside of urchins were much superior to those on the outside, and forthwith gave up free-living habits permanently."

Reading paragraphs at random, the reviewer came upon two points which deserve mention. On page 201 there is an erroneous statement to the effect that nothing is known about how the medusae of *Gonionemus* are produced, and on page 244 there is a curious statement about *Polyorchis:* "It swims beautifully and rather well by kicking the manubrium . . ." It is true that when this jellyfish swims there may be a jerking of the manubrium with each pulsation of the bell, but this jerking seems to be the result, not the cause of the movement of the animal.

In addition to the alphabetical index there is an annotated systematic appendix which is combined with an annotated bibliography.

Both the ecologist who would like to familiarize himself with some of the common invertebrates of the' Pacific Coast, and the invertebrate specialist who needs to get away from the phylogenetic viewpoint and look upon invertebrates in relation to habitat and as members of a community, will want to have this book.

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ROOT NODULE BACTERIA AND LEGUMINOUS PLANTS [1]

The monograph on *Root nodule bacteria and leguminous plants,* by Fred, Baldwin, and McCoy, appeared in 1932. Since then, as the authors point out, interest in this field has increased, and many important investigations dealing with the characteristics of the leguminous plants, and of the bacteria associated with them, have appeared. Greater emphasis has been placed on the physiology of the

[1] Fred, Edwin Brown, Ira Lawrence Baldwin, and Elizabeth McCoy. 1939. Supplement to root nodule bacteria and leguminous plants. *The University of Wisconsin Press, Madison.* 50 cents.

plant bacterial association, on the mechanism of nitrogen fixation, the excretion of nitrogenous compounds from the leguminous plants, and cross-inoculation. The present *Supplement* is a bibliography of the papers published from 1932 to 1938, and a few titles not listed in the 1932 monograph. The *Supplement* includes an "Index to scientific plant names," and an "Index to author citations," both by Dr. O. N. Allen and Ethel K. Allen. This is an invaluable publication for all students and investigators of this subject.

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

## LIFE AND ENVIRONMENT [1]

Life and Environment is the first volume to appear in a "series of basic science materials" to be published under the auspices of the Bureau of Educational Research in Science, of Teachers College, Columbia University. It is an interpretation of situations and problems arising out of the interrelations between human society and its living and non-living environment. The volume presents in broad relations a survey of man and his society. "Plants, animals (including man), soil, air, rain, heat, cold, fire, wind, are compounded into a comprehensive and ever changing world-picture. In viewing this picture the reader may identify the changes in progress and in turn may direct his efforts so as to advance those that are constructive and so as to arrest those that are destructive."

The book supports the theses that life and environment are inseparable except for purposes of analysis, and that the development of our knowledge of environment is a phase of advancing human culture. The main divisions of environment include not only the lithosphere, hydrosphere, and atmosphere, but also the biosphere which includes human society as the immediate living environment of the individual human being. Ecology is defined as "the testing and synthesis of whatever can be known about life and environment, in order to interpret their relationships in scientific terms." The last chapter (VIII) treats of the social function of society, which is "to provide a scientific basis whereby man may shape the environment and his relations to it, as he expresses himself in and through his culture pattern." The Appendix gives suggestions as to the use of this material in teaching, and as to collateral reading. In a stimulating way the book opens up wide vistas as to the scope of ecology and its relation to our daily lives.

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

[1] Sears, Paul B. 1939. Life and environment. xx + 175 pp. *Bureau of Publications, Teachers College: Columbia University, New York.*

# BOOK NOTICES

**Baker, F. C.** 1939. Fieldbook of Illinois Land Snails. *Ill. Nat. Hist. Survey Div., Manual 2, Urbana, Ill.* 166 pp., illstr., col. frontispiece. This book is a fine systematic account, well illustrated, of the land molluscs of Illinois. Advice to collectors and to classifiers is given in addition to the keys, descriptions of the species, check list, bibliography and index. It is a model of a handy book dealing with an important group of animals in the fauna of this state.

**Metcalf, C. L., and W. P. Flint.** 1939. Destructive and Useful Insects, their habits and control. 2d ed. *McGraw-Hill Book Co., N. Y. and London.* 981 pp., 584 figs. $7.50. The second edition of this well known book has appeared about ten years after the first edition. The work has been rewritten in a large measure with much new material added. Keys to orders of insects include keys to larvae and pupae. Anatomy, physiology, classification and control are dealt with at length. About two-thirds of the book is divided into chapters upon the plants and ecological habitat infested. Under each economic group of plant pests, the order of presentation is ecological. A useful cross-reference system is used throughout the work in addition to a good index. The size and arrangement of this book, as well as the care and accuracy of presentation, make it the best reference work in its field.

**Morgan, Ann Haven.** 1939. Field Book of Animals in Winter. *G. P. Putnam's Sons, New York.* 527 pp., 283 figs. and pls. $3.50. This is a well illustrated and handy field manual which should stimulate field studies in winter and make winter ecological studies more interesting and satisfactory. The chapters include a study of general winter activity, migration, hibernation, and the effect of the winter season upon land and fresh-water communities. The body of the book is devoted to a study of the winter habits of the various phyla and classes of animals with much interesting ecological observation upon each group. There is a good bibliography and the book is well indexed.

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# NOTES AND COMMENT

## THE EFFECT OF EXPERIENCE ON FIGHTING BEHAVIOR OF ALBINO MICE

In a paper published recently [1] the following conclusion, among others, was reported based upon the observation of approximately 300 males and 150 females over a period of two years:

The home cage seemed to have a strong favorable effect on the fighting success of the albino mouse.

In connection with this result, males were sometimes paired for usually from one to two hours in pens new to both individuals. The possibility that previous experience may effect the reaction of one male toward another in this

[1] Uhrich, J. 1938. The social hierarchy in albino mice. *Jour. Comp. Psych.* 25: 373–413.

paired condition seemed sufficiently important to justify this further analysis.

Only those pairs are here considered in which both individuals were normal adults and were meeting for the first time in a cage that was the home environment of neither. Fifty pairs met these conditions. Of these, no fighting was observed in fifteen cases. In nine of the remaining 35 pairs one or both individuals had had no previous experience with strange males in a strange pen; there were then 26 pairs in which both males had had previous contact with strange males in a pen new to both. These 26 pairs actually involved 20 males, since each indvidual was used in from one to seven pairs.

TABLE I. *Showing the social status of each male mouse in his own group, the relative weight and age, and the previous experience of each victorious and defeated member of 26 pairs of albino mice*

| Pair Number | Social status in group | | | | Relative weight | | | Relative age | | | Previous experience | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dominant | Subordinate | Unsettled | No fighting | Lighter | Heavier | Similar | Younger | Older | Similar | No fighting | Victorious | Defeated |
| 1 | — | — | V d | — | — | — | — | — | — | V d | V d | — | — |
| 2 | — | V | d | — | — | — | V d | V | d | — | — | V d | — |
| 3 | — | d | V | — | — | — | V d | d | V | — | — | V d | — |
| 4 | — | V | d | — | — | — | V d | V | d | — | — | V d' | — |
| 5 | V | — | d | — | d | V | — | V | d | — | — | V d | — |
| 6 | — | V | d | — | — | — | V d | V | d | — | — | V | d |
| 7 | — | d | V | — | — | — | V d | d | V | — | — | — | V d |
| 8 | — | V | d | — | d | V | — | V | d | — | V d | — | — |
| 9 | V | — | d | — | d | V | — | V | d | — | — | V | d |
| 10 | — | V | d | — | d | V | — | V | d | — | V d | — | — |
| 11 | — | d | V | — | — | — | V d | d | V | — | d | V | — |
| 12 | — | d | V | — | — | — | V d | d | V | — | — | V d | — |
| 13 | — | — | d | V | — | — | V d | — | — | V d | d | V | — |
| 14 | — | — | d | V | d | V | — | d | V | — | — | V d | — |
| 15 | — | — | d | V | — | — | V d | d | V | — | — | V d | — |
| 16 | V | — | — | d | — | — | V d | — | — | V d | — | — | V d |
| 17 | — | — | — | V d | — | — | V d | d | V | — | — | V d | — |
| 18 | — | V | — | d | — | — | V d | — | — | V d | — | V d | — |
| 19 | — | V | — | d | V | d | — | V | d | — | — | V | d |
| 20 | — | d | — | V | — | — | V d | d | V | — | — | V | d |
| 21 | — | V | — | d | d | V | — | V | d | — | — | d | V |
| 22 | V | — | — | d | — | — | V d | V | d | — | — | V d | — |
| 23 | d | — | — | V | — | — | V d | d | V | — | — | V d | — |
| 24 | V | — | — | d | — | — | V d | V | d | — | — | V | d |
| 25 | — | — | — | V d | — | — | V d | — | — | V d | — | V | d |
| 26 | — | — | — | V d | — | — | V d | — | — | V d | — | V | d |
| V | 5 | 8 | 5 | 8 | 1 | 6 | 18 | 11 | 9 | 6 | 3 | 20 | 3 |
| d | 1 | 5 | 11 | 9 | 6 | 1 | 18 | 9 | 11 | 6 | 5 | 12 | 9 |

* V—Victorious. d—defeated.

Most males were between 100 and 200 days old; one was as young as 95 days; five exceeded 300 days, and one was over a year old. In weight they varied from 18 to 31 grams, but ranged mainly between 24 and 27 grams. The time of elapse since the last previous experience was 10 days or less. In 18 pairs the interval was 1 to 3 days, in one less than 1 day, and in 7 it was 4 to 10 days. The time of elapse was the same for both members in 21 pairs; in five cases there was a difference of 1 to 6 days between the opponents. Table I summarizes the experiments.

The social status of each male is classified as (a) dominant over the pen mates, (b) subordinate to some, (c) unsettled order, that is with some fighting but with no male as the despot, (d) no fighting apparent. If the opponents differed by 5 grams or more from each other, they were classified as heavier and lighter, otherwise they were classified as of similar weight. No weight record on the first pair was available. In those pairs in which the younger individual was between 90 and 180 days old and was at least 30 days younger than his opponent, they were classified as younger and older, otherwise they were regarded as of similar age. In regard to the last previous experience with a strange male in a pen new to both, each mouse was classified as: (a) no fight observed, (b) victorious, (d) defeated.

An examination of table I shows that most males were subordinates in their own pens or came from groups in which the social order appeared unsettled or no fighting was observed. The ratio of 5 victories to 1 defeat among the dominants suggests a positive correlation between a combatant's social position in his own group and his success in these paired fights. The ratio of 8 victories to 5 defeats among subordinates is the reverse of the results expected on the basis of this suggestion. It will be noted, however, that the subordinates were tested against mice from cages in which the social order was unsettled either because of inconclusive fighting or because of its absence. The ratio of 5 victories to 11 defeats among those coming from unsettled groups is not explicable at present.

In 18 pairs the opponents differed in weight by less than 5 grams. Of the 7 cases in which there was a difference of 5 or more grams, the lighter individual won 1 and lost 6 combats. In these 7 pairs relative weight may have been one of the factors determining the outcome of the fight. Relative age appears to have been of practically no importance.

Previous experience, more than any of the preceding factors, appears to have been of some importance in the outcome of these fights. Twelve previous defeats resulted in 3 victories and 9 defeats, or a ratio of 1 victory to 3 defeats; 32 previous victories resulted in 20 subsequent victories and 12 defeats, or a ratio of 5 victories to 3 defeats. This suggests a positive correlation between previous success and subsequent victory.

Because of the small number of examples and the presence of several other variable factors in some cases, such as social status and weight, a more definite conclusion would be unwarranted.

The results, however, indicate that an extensive, well controlled attack on this problem of the effect of previous success or failure on the outcome of subsequent combats in mice would yield some very interesting results.

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## AUTECOLOGY OF THE GOLDEN-ROD GALL FLY

The gall produced on various species of Golden-rod by the fly *Eurosta solidaginis* Fitch is remarkable because of the great thickness of tough, pith-like cells which compose it, and because most naturalists are well acquainted with it. Each gall is a spheroidal swelling on the main stem of the plant, usually near the top. It often becomes more than one inch in diameter, and is a conspicuous object on dead, but still erect, plants during the winter months. A single larva inhabits each gall, living in a spherical chamber at the center. It pupates in early spring, and in the period from April until June, emerges from the gall by pushing open a circular door through the epidermis at the end of a radial tunnel excavated during the last larval instar.

Because these galls are easily obtainable during the winter months, and each is occupied by a single larva, they constitute ideal material for studying the ecological relationships of gall flies. Gall flies present especially interesting problems, since, of the many niches occupied by animals, few would seem to offer more protection than that in the center of hypertrophying plant tissue.

The biotic potential of an insect such as the Golden-rod gall fly must be considered to consist of the viable eggs which one female can lay during the single, short season of adult life. Dissection of ten virgin females indicates that in this species the average number of eggs is in the neighborhood of seventy-five ($73.4$, $\sigma_{mean} = 0.9$, $\sigma_{counts} = 2.7$). The likelihood of their

being fertilized would depend upon the availability of males. Scarcity of mates is probably not important in limiting the reproduction of the fly, since of ninety-eight specimens which successfully emerged as adults, sixty-two (63.3 per cent) were males, and the population is reasonably dense in infected areas (see below).

The environmental resistance of this insect is composed of many separate factors. One which was thought to have little effect on the number of insects reaching maturity was lack of healthy Golden-rod plants of the proper species at the time of ovipostion, since wherever *Solidago canadensis* L. was found in waste acreage, it was both abundant and not over thirty-five per cent attacked (see below). No evidence is available at present to indicate that plants free from galls are so because no eggs were deposited on them. Immunity from attack is quite possible, perhaps taking the form of absence of reaction to the hypertrophic stimulus provided at the time of oviposition. Since there is no way to evaluate the eggs deposited where they are unable to develop, it has been necessary

for the present discussion to assume that galls resulted from all eggs which the female was able to lay. Whatever error is inherent in this procedure will be a factor in the environmental resistance to the insect.

For the purposes of this study, five sample plots were selected in which *Solidago canadensis* was common. Of these plots, none were closer together than one half mile, none farther apart than fifteen miles. All plots consisted of a larger area than one acre, so that the appearance of the particular Golden-rod was that of a plant successfully holding its own among the other vegetation. The plots represented a variety of situations—forest edge on level ground (Plot 1), exposed hillside (Plot 2), open ravine protected from wind by trees on the rim (Plot 3), lake margin (Plot 4) and level, undeveloped city lots (Plot 5). From each of these plots, two hundred Golden-rod stalks were collected, the stalks selected being adjacent to one another and all at least three feet high, and hence well exposed all winter above the snow. Fifty galls were selected at random in each of the five

TABLE I. *Mortality analysis of populations of the Golden-rod gall fly*

| | Plot 1 | Plot 2 | Plot 3 | Plot 4 | Plot 5 | Summary |
|---|---|---|---|---|---|---|
| Stalks collected | 200 | 200 | 200 | 200 | 200 | 1,000 |
| Number with galls | 42 | 57 | 50 | 62 | 53 | 264 |
| Per cent infestation | 21.0 | 28.5 | 25.0 | 31.0 | 26.5 | |

Mean infestation 26.4%, $\sigma_{mean} = 1.7\%$, $\sigma_{plots} = 3.4\%$

| | | | | | | |
|---|---|---|---|---|---|---|
| Galls selected | 50[1] | 50 | 50 | 50 | 50 | 250 |
| Killed by birds | 21 | 22 | 22 | 23 | 24 | 112 |
| Per cent killed by birds | 42.0 | 44.0 | 44.0 | 46.0 | 48.0 | |

Mean killed by birds 44.8%, $\sigma_{mean} = 1.0\%$, $\sigma_{plots} = 2.0\%$

| | | | | | | |
|---|---|---|---|---|---|---|
| Emerged in laboratory | 21 | 19 | 21 | 18 | 19 | 98 |
| Per cent emergence | 42.0 | 38.0 | 42.0 | 36.0 | 38.0 | |

Mean emergence 39.2%, $\sigma_{mean} = 1.3\%$, $\sigma_{plots} = 2.4\%$

| | | | | | | |
|---|---|---|---|---|---|---|
| Males | 13 | 12 | 14 | 11 | 12 | 62 |
| Females | 8 | 7 | 7 | 7 | 7 | 36 |
| Per cent males | 65.0 | 63.2 | 66.6 | 61.2 | 63.2 | |

Mean proportion males 63.3%, $\sigma_{mean} = 0.3\%$, $\sigma_{plots} = 1.9\%$
Mean proportion females 36.7%, standard deviations the same

| | | | | | | |
|---|---|---|---|---|---|---|
| Unemerged on May 11 | 8 | 9 | 7 | 9 | 7 | 40 |
| Per cent unemerged | 16.0 | 18.0 | 14.0 | 18.0 | 14.0 | |

Mean failure to emerge 16.0%, $\sigma_{mean} = 0.3\%$, $\sigma_{plots} = 1.8\%$

| | | | | | | |
|---|---|---|---|---|---|---|
| Killed by beetles | 2 | 1 | 1 | | | 4 |
| Killed by parasites | | 2 | 1 | | 1 | 4 |
| Fungus in gall cavity | | | | 1 | | 1 |
| Dead as adult | 1[2] | 2[3] | | 1[3] | | 4 |
| Dead emerging | 1 | | | | | 1 |
| Dead as late pupa | | 2 | | 1 | 1 | 4 |
| Dead as early pupa | 1 | | 1 | 2 | 1 | 5 |
| Dead as young larva | 3 | 2 | 4 | 4 | 4 | 17 |

[1] — additional stalks collected until 50 galls had been obtained.
[2] — before partly opened door.
[3] — no exit passageway prepared by larva.

sample plots. In each of these gall groups, a number were noted which had been attacked by birds, presumably woodpeckers and nuthatches, and in all but four, the wide conical crater made by the bird reached the insect's cavity at the gall center and the chamber was empty. The four galls attacked by birds but not completely opened produced flies in the laboratory. The collected galls were kept in cages at 70° F. from the time of their collection (April 5) until there seemed little likelihood of further emergence. While a wet sponge was kept in the box with the galls throughout their laboratory experience, there is no proof that emergence in the field would have been of identical percentage with that observed indoors. Humidity is probably of importance. One month less of cool weather with great variation in temperature may have affected the emergence also.

The details of emergence or time of death in each of the plots is indicated in table I.

In the autopsy held on May 11, none of the forty unemerged galls was found to contain living *Eurosta*, and the data obtained were very miscellaneous. Seventeen had died as young larvae with no cause apparent in the gall. All five plots showed approximately the same mortality at this stage. It is interesting to note that these galls were not different in size or shape from those in which the life cycle had been completed, indicating clearly that the hypertrophic stimulus is provided the plant only at the beginning of larval life, perhaps by the parent fly, but more probably by the very young larvae, since uninhabited galls were not found. This fact is in distinct contrast to the findings of Molliard[4] and Vorms[5] on the beech gall caused by *Mikiola fagi* Hartig, in which hypertrophy ceased and the characteristic pigmentation of the gall did not develop if the larva were killed by an incision or affected by a parasite. Five had died as early pupae and four others as late pupae. Two died emerging from the puparium, one never having freed itself from the amnion, the other shrivelled in the exit passage before a partially opened door. Three died as adults from starvation inside the gall, not having been provident enough as larvae to bore an adequate passageway to the gall's epidermis. All of the above might be classed as deaths inherent in the species, perhaps resulting from the action of lethal genes. They total

thirty-one specimens (12.4 per cent of the original two hundred and fifty galls).

External influences accounted for the death of eight of the nine specimens remaining (3.6 per cent). One had died in the puparium and the gall cavity was filled with a mold in fruition, identified as an *Aspergillus* species. There was no proof that the fungus caused the death of the insect, nor was any means of ingress for the fungus discovered. Four specimens had been killed in the puparium by predaceous beetles of the family Mordellidae, which burrow into the galls from the Golden-rod stalks, via the vascular tissue. In three of the four instances, the beetle was captured and proved to belong to genus *Mordellistena*. The gall cavity following the ravages of these beetles was completely filled with gray powder. The residual four specimens were parasitized as larvae by Hymenoptera of the genus *Eurytoma* (Eurytomidae). These leave the gall shining inside with a resinous material, perhaps by a byproduct of the final disintegration of their hosts. Of the four parasites, one died in early pupal life prior to May 11, two had emerged but were unable to leave the gall chamber and had died there, supposedly from starvation, also before May 11. The remaining specimen was a teneral pupa, white with white eyes, which eventually darkened and emerged (July 3) as a large female. Like the others, it had killed its host before any passageway was excavated to the epidermis of the gall, and consequently would not have been able to escape. Perhaps this is a case of parasitism in error, the host of the specific *Eurytoma* being properly a different insect than *Eurosta solidaginis*. The difference in the appearance of the gall chamber of those specimens killed by hymenopterous parasites from the dust-filled condition after activities of mordellid beetles, was striking. *Eurosta* leaves its chamber clean and dry, with neither dust nor resin. It is to be noted that parasitism of *Eurosta* by *Eurytoma* does not cause an acceleration of development and early pupation as was found in several gall-formers by Varley and Butler.[6]

On the basis of an average biotic potential of seventy-five viable eggs per female per year (see above), the environmental resistance quantitatively studied would account for the death of sixty-one (60.8) per cent, or about forty-six (45.8) eggs. Of the remaining thirty-nine per cent (twenty-nine eggs), an expectancy of sixty-three per cent males (see above) would leave to the hazards of adult life only eleven (10.7) females. For the species to remain at the same population level, ten of these females (and probably also eighteen males) must be

[4] **Molliard, Marin.** 1926. Dimorphisme déterminé chez la galle de *Mikiola fagi* Hartig par un parasite secondaire. *Compt. Rend. Acad. Sci. Paris* **183** (16) : 624–626.

[5] **Vorms, Mme.** 1933. Caractères anatomiques résultant de l'arrêt du développement chez les galles. *Compt. Rend. Acad. Sci. Paris* **196** (8) : 558–560.

[6] **Varley, G. C., and C. G. Butler.** 1933. The acceleration of development of insects by parasitism. *Parasitology* **25** (2) : 263–268.

destroyed, or their progeny prevented from developing galls, leaving one female (and perhaps also one male) to successfully lay the seventy-five fertile eggs provided her. No data are available at present to explain the fate of these individuals, although a number of possibilities present themselves. Immunity on the part of Golden-rod plants has already been suggested, and any factor preventing the complete and successful mating of the flies would seriously affect their numbers in the community. The Golden-rod gall fly is a member of the family Trypetidae, the pairs of which perform a complicated, wing-waving, gyrating dance prior to copulation. A break in the continuity of this display upsets the pair, usually resulting in their flying away in different directions and not returning to complete the act. That the dance requires several minutes before copulation takes place, and that disturbance causes its termination without results, leads one to believe that such a behavior pattern lends itself readily to interruptions, and hence reduces the likelihood of the female's eggs being fertilized. Moreover, the statistics cited above are based on galls collected in early April. It is not unlikely that birds and beetles would have killed a portion of this small group before they emerged, had they been left in the field rather than protected in the laboratory. Those which survived to emerge would brave birds and other predators, uncertain weather conditions typical of early spring, and similar hazards which could readily reduce them to the regular residue of one adult functioning pair from the progeny of each pair

of parents. For the population level to remain constant within narrow limits, the ratio of biotic potential to environmental resistance must average unity. It is of course very unlikely that a female will lay her full quota of eggs before accident overtakes her, the several survivors together being necessary to place the collective offspring on succulent young Golden-rod plants, thus expressing the total biotic potential as determined for the species. It is also quite within the realms of probability that not all of the young Golden-rod plants on which eggs were successfully placed would survive long enough for the gall fly to complete its development. Nalepa[7] found that there were many factors which affected the growth of the plant enough to alter the gall population, and explained on this basis much of the variable occurrence of galls. In the one year when the present survey was made, little difference is observable which can be related positively to the habitat in which the Golden-rod grew. Perhaps the factors which affected the gall population through their host plant are more of the type which would concern all members of the plant species irrespective of the place in which they grew.

Since few niches are as well protected on all sides as that in the center of hypertrophying plant tissue, it is very interesting that scarcely over one third of the progeny of each female survives the gall-inhabiting stage. This fact

[7] Nalepa, A. 1928. Zur Phaenologie und Entwicklungsgeschichte der Milbengallen. *Marcellia* 24: 87–98.
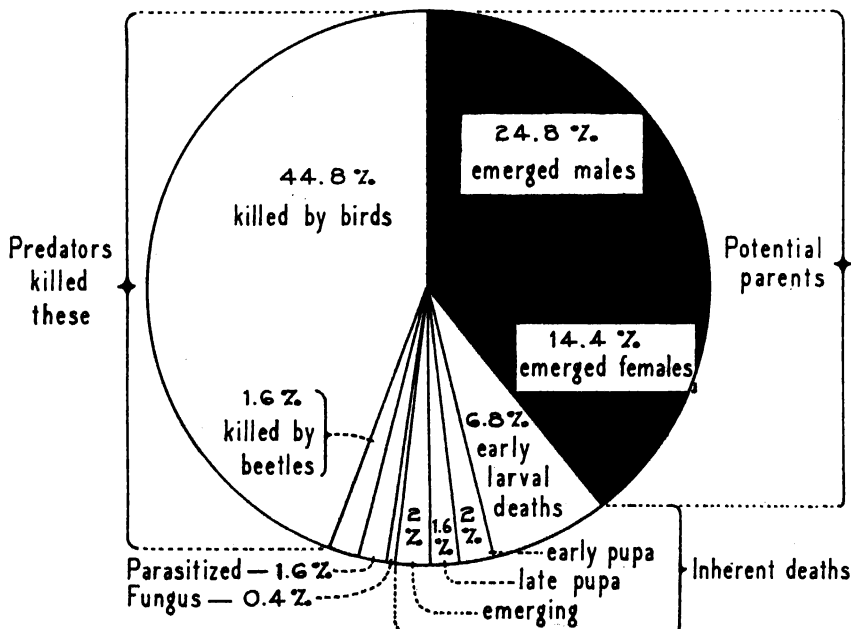


FIG. 1. Mortality and survival of Golden-rod gall fly populations.

does not lend support for Wolff's [8] contention that the protection provided the larva by the plant is so complete that the gall-maker does not need many eggs since most of them will reach maturity, and that in this way the plant actually reduces the number of hypertrophic growths which it is called upon to make. The low rate of parasitism (1.6 per cent) and the high incidence of attack by birds (44.8 per cent plus the unsuccessful 1.6 per cent totals 46.4 per cent actual molestation) is undoubtedly related to the conspicuous, if rather resistant, habitat in which the insect spends so much of its life cycle. The accompanying circular dia-

gram (fig. 1) sums up in graphic form the fate of the progeny of the Golden-rod gall flies which developed galls. If all the females which emerged were to live to reproduce, the environmental resistance would be inadequate to restrain the species from a sudden increase in population. The precise percentage which actually does reproduce *must* be much less, since such an increase does not occur. The unmeasured environmental factors discussed unquestionably account for a substantial reduction.

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## THE CARDIO-VIBROMETER: A NEW INSTRUMENT FOR MEASURING THE HEART RATE AND OTHER BODY ACTIVITIES OF ANIMALS [1]

In higher animals the rate of heart beat is generally recognized as being a sensitive index to the physiological condition of the whole animal. Although much studied in man, the heart rate of most mammals and birds, particularly wild species, is little known because of the difficulty of measuring it, as by subcutaneous needle electrodes, without greatly disturbing the animal. The purpose of this communication is to give a brief description of an apparatus that will accurately determine the heart rate under a variety of experimental and natural conditions with very little disturbance to the animal and which should prove useful in ecological investigations where the physiological state of animals under natural conditions needs to be determined. Results obtained in a study of the heart rate of birds will be presented in a subsequent paper.

The piezo-electric principle is utilized. Certain crystalline substances, particularly Rochelle salt (sodium-potassium-tartrate), have the property of producing a difference of electrical potential between opposite sides of the crystal proportional to the pressure applied and, conversely, of producing motion proportional to the difference of electrical potential applied to opposite sides of the crystal. By the use of such crystals and an amplifier, a system may be constructed whereby very slight variations in pressure, as by the slight motions or "jars" of the body produced by each heart cycle, can be picked up, amplified, and recorded on moving paper and the frequency determined. Thus, the apparatus has been named the "cardio-vibrom-

eter" or simply "vibrometer," literally, "an instrument recording vibrations."

Illustrations of the various modifications in the use of the pick-up as well as of the entire apparatus are shown in figure 1. The amplifier consists of three stages resistance capacity coupled and is adapted to respond to low frequencies. A variable resistor (9) across the input controls in some measure the frequency response. A high resistor setting seems to give the best recording with birds, as very low frequency movements, such as the swaying of the perch, tend to be reduced in the graphic records. However, a low setting may be useful in recording movements due to breathing. A pair of crystal earphones (14) are attached across the output so that it is possible to listen to the heart beat and movements of the animal. The amplifier operates on ordinary 110 volt house current, is enclosed in a case 12 × 7 × 7 inches, and weighs about five pounds.

The recorder weighs about ten pounds and is enclosed in a case 13.5 × 6.5 × 6 inches. The amplified current from the pick-up crystal passes through a large crystal in a sealed case (16) which drives a light aluminum pen (18). Thus, every movement on the perch is duplicated in amplified form by the pen, which will respond to vibrations of 0–90 per second, more than ample to record all ranges of heart rate. The paper drive (20) is operated by a 60-cycle synchronous motor. Consequently the paper speed is very uniform and no timer is necessary. There is, however, room for two pen motors in the recorder so that two records can be made simultaneously or one pen can be used as a timer. Two paper speeds are available; the speed of 2 inches per second is quite ample for the usual range of heart rate of small birds and mammals (200–800 per minute), while the speed of 6 inches per second is useful for very rapid rates of excited birds (which may run over

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[8] **Wolff, Gustav.** 1927. Zur Frage der "Fremddienlichen Zweckmässigkeit." *Zeitsch. Wiss. Biol. Abt. D, Wilh. Roux' Arch. Entw. Org.* 111 (1): 435–452.

[1] Contribution No. 35 from the Baldwin Bird Research Laboratory, Gates Mills, Ohio.
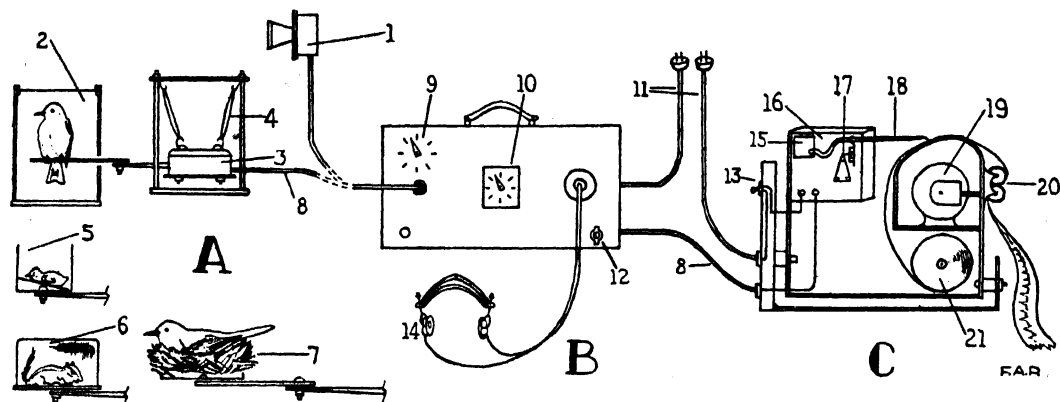
FIG. 1. The cardio-vibrometer. (*A*) Pick-up units, (*B*) amplifier, (*C*) pen recorder; (1) stethoscope type direct pick-up for animals held in the hand, (2) container for small perching birds, (3) pick-up crystal in metal case for electrical shielding, (4) rubber suspending bands, (5) container for nestling birds with the sloping bottom imitating the natural concavity of the nest, (6) container for small mammals, chicks, or non-perching birds, (7) arrangement with an incubating bird at the nest, (8) shielded connecting cables, (9) variable resistor control, (10) gain or amplification control, (11) 110-volt power inputs, (12 and 13) switches, (14) crystal earphones, (15) ink well, (16) recording crystal, (17) pen drive mechanism, (18) recording pen with glass writing point, (19) synchronous paper drive motor, (20) paper drive (gears not shown), (21) paper roll of type used in adding machines.

1000 per minute). A great advantage of such a pen recorder over the usual photographic recorder is that records are immediately available without expensive and time-consuming film development. The apparatus should be grounded, preferably both at the pick-up and at the amplifier. The cable (8) connecting the pick-up unit and the amplifier is long enough to allow placing the pick-up and the animal in one room and the amplifier and recorder in another or in a nearby blind. Excessive moisture or high humidity around the crystals should be avoided as well as temperatures above 115° F.

Typically, there is a sharp peak deflection or a diphasic wave with each heart cycle, apparently coinciding with the systole. In small birds this amounts to one-half to one inch in the record using only one-half the possible gain of the amplifier. Sometimes, but not usually, there is a second peak resembling the second heart sound, but in general the curve does not permit analysis like an electrocardiogram. The form of the curve varies a good deal according to the animal, its position on the crystal perch, and the setting of the amplifier. The heart beat, unlike other movements that may be recorded, is normally quite regular, so that with practice it is easily distinguishable.

Heart rate can only be determined with the vibrometer when the animal is quiet but this is usually desirable anyway. The use of the apparatus for recording heart rate is limited only in very small animals or where the force of the beat in proportion to the size of the body is very weak or where other movements interfere to too great an extent. The heart rate and movements of the embryo in the unopened egg have

been obtained. In addition to heart beat, the rate of breathing can often be simultaneously recorded. The vibrometer furnishes a means of recording muscle tremors, such as are important in temperature regulation, even when shivering is not perceptible. At low air temperatures, the recording of heart rate is obscured by the intensity of these tremors. Preliminary attempts have been made to record rate of wing beat in hummingbird and insect. The vibrometer will also serve as a recorder of general activity of animals by which not only the duration but to some extent the degree of activity may be determined. Undoubtedly, many other uses will develop with time.

The authors are indebted to Dr. S. Prentiss Baldwin, recently deceased, for helpful suggestions, to Mr. Roscoe W. Franks for his work with a preliminary form of the apparatus, and to Mr. C. H. Tower and Mr. Joseph J. Neff of the Engineering Department of the Brush Development Company, Cleveland, Ohio, who designed the amplifier and largely built the apparatus.

Further details on the properties of Rochelle salt crystals and on the construction of the pen recorder may be obtained from "Data Sheet, Numbers 1 and 2" and "Engineering Bulletin Number 110" published by the Brush Development Company.

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# A Simplification of Powers' Method for the Determination of Carbon Dioxide in Natural Waters and Comparison with the Titration Method

The method of Powers [1] for determining carbon dioxide in natural waters consists in finding the pH of the water as it naturally exists and, in addition, finding it at two specific carbon dioxide levels. From these data, using ionization constants, and air-water carbon dioxide ratios the carbon dioxide content is calculated.

This paper introduces temperature corrections and shortens the calculations by means of tables. The variation of $pK_1$ with temperature is significant, and to avoid error from this source we have plotted the values against temperature from the data of Shedlovsky and MacInnes [2] and from the curve read off the values of $pK_1$ at 5° intervals from 0° to 40° which are given in table I. The temperature is important for if a value of $pK_1$ for 25° is used in place of the proper value at 20° the amount of carbon dioxide in parts per million is decreased 7 per cent.

TABLE I. *The variation of $pK_1$ with temperature*

| Temperature °C. | $pK_1$ | Differences |
|---|---|---|
| 0* | 6.583 | |
| | | 130 |
| 5 | 6.453 | |
| | | 81 |
| 10 | 6.472 | |
| | | 42 |
| 15* | 6.430 | |
| | | 36 |
| 20 | 6.394 | |
| | | 29 |
| 25* | 6.365 | |
| | | 22 |
| 30 | 6.343 | |
| | | 17 |
| 35 | 6.326 | |
| 38* | 6.317 | 15 |
| 40 | 6.311 | |

* Original data.

Carpenter [3] states that the carbon dioxide content of the air is .031 per cent and remarkably constant. We have used this figure in the calculations.

For determining pH we have used both indicators and the glass electrode. When using indicators we find the LaMotte Hydrogen Ion Testing set, 3R, satisfactory. This set uses small cups holding about 1 ml. We find we are able to detect differences of .1 and possibly .05 pH units. If the glass electrode is used all the measurements must be made on this instrument. The field reading cannot be made with indicators and the other readings with the instrument. An individual colorimetric reading may not agree with the glass electrode, but if all the readings are made in one way the errors tend to cancel.

The calculations in this method deal mostly with constants, the temperature being the only variable; if then the data can be assembled as factors, varying with temperature; the calculation will be much simplified. Such data are assembled in table II.

TABLE II. *$X_1$ and $X_2$ values for the determination of n*

| Tempera- ture °C. | Values for X | |
|---|---|---|
| | Aerated $X_1$ | Alveolar $X_2$ |
| 0 | 11.21 | 8.95 |
| 5 | 11.24 | 8.98 |
| 10 | 11.27 | 9.01 |
| 15 | 11.30 | 9.05 |
| 20 | 11.34 | 9.08 |
| 25 | 11.38 | 9.13 |
| 30 | 11.43 | 9.17 |

In this table $X_1$ and $X_2$ give values of factors from atmospheric and alveolar equilibria to be used in obtaining $n$ values from the relationship $pH/x = n$. The equations used follow the work of Powers and Bond [1] and are here given:

$$X = pH_1 - \log \alpha + \log \left( 22.4 \frac{273 + T}{273} \right) - \log PCO_2$$

$$n = - pK + \frac{- pH}{\log \alpha - \log \left( 22.4 \frac{273 + T}{273} \right) + \log PCO_2} = \frac{pH}{X}$$

$\alpha$ = ratio $CO_2$ in air/$CO_2$ in water.

[1] Powers, E. E. 1927. A simple colorimetric method for field determinations of the carbon dioxide tension and free carbon dioxide, bicarbonates and carbonates in solution in natural waters. I. A theoretical discussion. *Ecology* 8: 333–338. II. Powers, E. E., and J. D. Bond. 1927. A critical mathematical analysis of theory and data. *Ecology* 8: 471–479; 9: 364–365.

[2] Shedlovsky, T., and D. A. MacInnes. 1935. The first ionization constant of carbonic acid, 0 to 38°, from conductance measurements. *Jour. Amer. Chem. Soc.* 57: 1705–1710.

[3] Carpenter, T. M. 1937. The constancy of the atmosphere with respect to the carbon dioxide and oxygen content. *Jour. Amer. Chem. Soc.* 59: 358–361.

*Theoretical.*—The $e$ in the equation pH = $-n$ (log $(Kk_{gas}$ P) $+ e$) of Powers and Bond [1] has disappeared. It covered the variations with temperature of $K$ and $k_{gas}$ as well as other errors. The temperature differences are covered in tables I and II as noted; the other errors would be the effect of solutes other than carbonic acid, and the incomplete hydration of carbon dioxide. However, solving for $e$ may introduce an error greater than the correction if too much stress is laid on the accuracy of the figures obtained from the alveolar equilibrium as any error in the measurement of alveolar pH will appear in $e$. Howell [4] cites two authors who give the carbon dioxide content of alveolar air as 5.3 and 5.6 per cent respectively, a difference of 5 per cent. Apparently some individuals, acting as analysts, will have the proper alveolar carbon dioxide concentration to check the air equilibrium and others will not be so favored. On the other hand the carbon dioxide content of air is remarkably constant. Hence the authors advise using the value of $n$ obtained from the air equilibrium for calculation and the $n$ from the alveolar equilibrium for a check only.

PROCEDURE

*The First pH.*—The first pH is that of the water as it exists naturally. It is best taken in the field. If water is brought into the laboratory care should be taken that it does not warm up. A larger sample is less affected, naturally, than a small one. If a bottle is filled it should be completely filled. The temperature is noted.

*The Second pH.*—The second pH reading is taken after the water is in equilibrium with the carbon dioxide of the air. Our results show that equilibrium is established out of doors in 5–10 minutes, using an ordinary squeeze bulb. However one source of error is failure to work the squeeze bulb long enough. A more convenient method is to bring the water into the laboratory and use a filter pump to draw air through the water, the supply of air being taken through a glass tube a couple of feet out the bottom of a window. The air in the laboratory cannot be used for the carbon dioxide content is much higher than out door air, and variable as well. The temperature is taken after saturation is reached. Following the attainment of equilibrium out of doors the water may be brought into the laboratory for the pH reading, provided that the temperature change is slight and the time before reading short.

*The Third pH.*—To get the third pH air is blown from the mouth into the water in a small flask until the sample is saturated. The tem-

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[4] Howell, W. H. 1936. A text book of physiology for medical students and physicians. W. B. Saunders Co., Philadelphia.

perature of the water is noted. The pH is determined as previously.

CALCULATIONS

Calculate $n$, using the second pH and again using the third pH. These calculations should give the same figure. If $n$ from the second is smaller it generally means the water was not in equilibrium with the air, and consequently the aeration should be continued for a longer time.

When the two values of $n$ agree within a few parts per thousand the data are complete. The two values of $n$ are a check one upon the other. Only one value can be used. The operator may average the values for $n$ or he may select the one he thinks is better. Generally the air value is more reliable. Having the data the $CO_2$ is figured according to the sample calculation which follows.

SAMPLE CALCULATION

The original pH is 5.7 at 18°; the second pH is 6.75 at 20° C.; the third 5.4 at 23°.

The value of $n$ for the second pH is found with the aid of table II. In column 2 and at 20° $X_1$ equals 11.34; $n$ therefore equals 6.75/11.34 which is .595. For the third pH the value of $X_2$ is taken from column 3 at 23° and equals 9.11; $n = 5.4/9.11 = .593$.

The two values of $n$, .595 and .593, are close showing the results are reliable. The value .595 is preferable rather than the average because it was obtained from the air equilibrium.

Next find the value of $pK_1$ at 18° from table I. The value is 6.402.

Now substitute the known values in the equation,

log $(H_2CO_3)$ = $pK_1 - pH/n$
log $(H_2CO_3)$ = $6.402 - 5.7/.595$
$= 6.402 - 9.58$
$= 6.822 - 10$ or $4.80$ or $0.80 - 4$
antilog $.80 = 6.6$ and $- 4$ is $10^{-4}$ so
$H_2CO_3 = 6.6 \times 10^{-4}$.

Thus the $CO_2$ ($H_2CO_3$) in the water is 6.6 $\times 10^{-4}$ molar. To express this in parts per million multiply by 44,000 and the result is 29 p.p.m.

COMPARISON WITH THE TITRATION METHOD

A titration method for determining carbon dioxide, using phenolphthalein and 0.1N sodium hydroxide is recommended for biological use. In this method 100 ml. of water is brought to a pink, and the sodium hydroxide reading is a measure of the carbon dioxide. We have made 20 determinations by this method, the results of which are shown in table III. In the first 10 the results are meaningless. In these first 10

TABLE III. *Comparison of powers pH method with titration method, carbon dioxide concentration expressed in parts per million*

| Order of performance | Powers colori-metric method | Titration to lingering pink | Titration to permanent pink |
|---|---|---|---|
| | ml. | ml. | ml. |
| 1 | 10.8 | 6.5 | — |
| 2 | 36.3 | 31 | — |
| 3 | 4 | — | 10.7 |
| 4 | 34 | — | 52 |
| 5 | 32 | 29 | — |
| 6 | 15 | 20 | — |
| 7 | 2.3 | 6 | — |
| 8 | 2.3 | 4.6 | — |
| 9 | 15 | 17 | 33 |
| 10 | 10.3 | — | 17 |
| 11 | 10 | 15 | 19 |
| 12 | 29 | 25 | 32 |
| 13 | 15 | 15 | 20 |
| 14 | 15 | 14 | 18 |
| 15 | 42 | 48 | 60 |
| 16 | 29 | 24 | 29 |
| 17 | 15 | 16 | 23 |
| 18 | 25 | 23 | 37 |
| 19 | 29 | 30 | 39 |
| 20 | 7 | 3 | 13 |
| Total (11–20) | 216 | 213 | 290 |
| Total (11–19) | 209 | 210 | 277 |

experiments the operator was selecting a pink for an end point which would give an amount of carbon dioxide corresponding to the colorimetric result. In other words, he was standardizing the procedure by the pH method. After a certain end point color was decided upon the results obtained in the last 10 experiments, checked fairly well with those obtained by the pH work.

The end point selected was not a permanent red, but a "lingering pink"; a color that flashes all through the liquid and lasts one or two seconds. The last ten titrations indicate that the operator had decided on the right end point for while the individual results vary, frequently up to 50 per cent, the errors average out.

The manipulator ordinarily would run such titrations to a lasting pink. Were this done, as in the data shown in the right-hand column, the results would be 30 per cent higher than those obtained by the pH process. Experiments 7, 8 and 20 indicate that determinations of small amounts of carbon dioxide are subject to greater proportionate error than large amounts.

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## TOLERATION EXPERIMENTS BY ECOLOGY CLASSES

Of necessity the ecologist is concerned with toleration physiology. This discipline frequently provides the key to those factors, both physical and biotic, that control and limit the distribution of organisms. Patently, serious research in toleration experimentation is a program of first water. At the same time it is possible to introduce students effectively to this concept by directing them into certain laboratory experiments that they can conduct and evaluate for themselves. It is the purpose of the present note (1) to call attention again to the pedagogical and biological importance of this field, and (2), to outline techniques that are suitable for class prosecution. The authors hold no brief for the superiority of the experiments suggested. If the paper stimulates an improvement in approach to this essential problem it will more than justify the effort entailed. One word of caution is necessary. It should be emphasized that the experiments described here are *class experiments* and are not, in any sense, put forward as an adequate or critical *research* program.

For a number of years the classes in animal ecology at the University of Chicago have made a reasonably intensive survey of lotic and lentic environments. Specifically, students study the biotic communities of streams and vernal ponds from the physiographic, physical-chemical and biotic aspects. In contrasting these communities many similarities and differences are observed. An important question that invariably arises in the minds of all adequate students is this: why are some animals limited to ponds and others to streams? In short, what are the *causal* factors? Obviously, this question cannot be answered profoundly by a class. But it can be attacked and partially delineated by toleration experimentation. In the streams and ponds of the Chicago Area many crayfish are found. These are all members of the same genus, *Cambarus*. The usual species are *C. propinquus*, *C. virilis*, *C. diogenes*, *C. blandingii*, and *C. immunis*. Here then is a population of genus rank common to both habitats. If the crayfish are used as experimental material the general questions just asked can be put in this specific form. How do pond crayfish differ from stream crayfish in their ability to tolerate en-

vironmental extremes? How are these differences, if consistent, related to actual field distribution?

In setting up any toleration experiment the ecologist is immediately confronted by the question: what environmental variables shall be chosen and how shall they be varied? This, of course, is a matter of judgment. In general it seems best to select those factors that appear to be of importance in the field. In our classes we have tested the toleration of crayfish to reduced oxygen tension, increased acidity, increased alkalinity and heat. The experiments have been performed as follows. Four crayfish from either stream or pond are introduced into the experimental container. Little attention is given to the species although modifications of the experiment could easily take this interesting aspect into consideration. The emphasis, as already stated, is an ecological one; the contrast of indigenous stream with indigenous pond forms. The crayfish are matched by weight so

that a "pond-container" has approximately the same total biomass as a "stream-container." All crayfish are collected from the field of a late afternoon and used in the laboratory early the following morning. For apparent reasons it is advisable to use the organisms as soon as possible after they reach the laboratory.

For the oxygen test well-water was boiled to lower its oxygen tension and siphoned after cooling into Erlenmeyer flasks. Then the pond and stream crayfish were introduced into separate flasks and each container was covered with a thick collar of mineral oil. The latter effectively prevents the absorption of more oxygen. Oxygen concentration was determined by the Winkler method for each flask at the start of the experiment and at the time of death of the last animal. Each crayfish was removed as it died. It is obvious that this technique does not discriminate between death due to oxygen starvation and contamination. The pH tests were run in similar containers

TABLE I. *Results of oxygen toleration tests*

| Habitat | Species | Number and sex | | Oxygen tension cc. per liter | | Mean time of death (minutes) | | | | Mean±P.E. |
|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| | | Males | Females | Start | End | 1 | 2 | 3 | 4 | |
| Stream | C. propinquus | 28 | 8 | 3.1 | 1.0114 | 171.7 | 206.7 | 235.2 | 275.5 | 222.2± 7.04 |
| Pond | C. diogenes C. virilis | 9 17 | 16 6 | 3.1 | 0.8999 | 318.3 | 378.3 | 434.2 | 512.3 | 410.8±15.53 |

TABLE II. *Results of pH toleration tests*

| Habitat | Species | Number and sex | | Mean time of death (minutes) | | | | Mean±P.E. |
|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| | | Males | Females | 1 | 2 | 3 | 4 | |
| | | | | N/5 HCl | | | | |
| Stream | C. propinquus | 16 | 8 | 11.5 | 14.3 | 16.3 | 18.8 | 15.2±0.77 |
| Pond | C. diogenes C. virilis | 13 3 | 8 12 | 18.5 | 23.5 | 29.2 | 33.7 | 26.2±1.00 |
| | | | | N/5 NaOH | | | | |
| Stream | C. propinquus | 12 | 0 | 36.7 | 50.7 | 73.7 | 82.0 | 60.8±2.12 |
| Pond | C. diogenes C. virilis | 0 4 | 8 0 | 68.7 | 97.0 | 117.0 | 146.3 | 107.2±5.65 |

TABLE III. *Results of heat toleration tests.  All crayfish started in water at room temperature (22.9° C.)*

| Habitat | Species | Number and sex | | Mean time (minutes) and Mean temperature at death | | | | | | | | | |
|---------|---------|-------|--------|------|-------|------|-------|------|-------|------|-------|-----------|-------|
| | | | | 1 | | 2 | | 3 | | 4 | | Mean | |
| | | Males | Fe-males | Min. | Temp. | Min. | Temp. | Min. | Temp. | Min. | Temp. | Min. ±P.E. | Temp. |
| Stream | *C. propinquus* | 27 | 5 | 49.5 | 32.5 | 58.4 | 34.1 | 65.1 | 35.5 | 68.6 | 36.2 | 60.4±.39 | 34.6 |
| Pond | *C. diogenes* *C. virilis* | 9 0 | 4 19 | 66.6 | 35.5 | 76.9 | 37.6 | 85.7 | 39.5 | 92.6 | 40.4 | 80.4±1.9 | 38.2 |

with four pond and four stream crayfish introduced into N/5 hydrochloric acid and N/5 sodium hydroxide solutions.  The time of death for each crayfish was recorded.  The heat tests were conducted in beakers placed in a water bath with hot and cold water inlets. These were so regulated as to increase the water temperature *within* the beaker one degree Centigrade every five minutes.  As before, four stream and four pond *Cambarus* constituted the experimental unit and the death time of each individual was noted.

The results of the spring class of 1939 alone are reported in this paper although earlier data are in general agreement.  The accompanying tables summarize the total experience of the class.  *Table I* depicts the oxygen results; *Table II* the pH results, and *Table III* the heat results.  From an examination of Table I it is apparent that the stream crayfish died sooner and at a higher oxygen tension than did the pond crayfish.  In the pH tests Table II shows both pond and stream forms are more tolerant of increased alkalinity than acidity.  However, in each experiment the stream animals died on the average sooner than did the pond whether they were subjected to acid or alkali.  Also in the temperature experiments (Table III) the stream forms began to die earlier and at lower temperatures than the pond forms.  The endpoint "death" was considered immobility. These data have been analyzed statistically. In all cases the difference between compared means for stream and pond forms exceeded by six times or more the probable error of that difference.  This signifies that the greater ability of the pond forms to withstand the environmental stresses established in the experiments cannot be attributed to chance.  In short,

it appears to be due to a real biological differential between the two ecological types.

How do the students use these data?  After the class results have been aggregated and tested statistically the students are encouraged to draw any conclusions they think warranted.  Pedagogically, this is the crux of the exercise.  Essentially all students conclude that stream crayfish are physiologically different from pond crayfish; a fact really apparent from *a priori* reasoning without recourse to experiment.  The ecological importance of the experiment lies in that it stimulates the class member to correlate tolerance or physiological differences with observed field distribution.  Thus the crayfish of vernal ponds are subjected regularly in nature to wide oxygen and temperature changes while the stream forms live in an environment constantly high in oxygen and of relatively stable temperature.  These facts check with the results of the laboratory tests and suggest that low oxygen and high temperature are important limiting factors for stream *Cambarus*.  The pH experiments are entertaining since they substantiate the well-appreciated ecological dictum that organisms eurokus for one factor tend to be eurokus for many; and *vice versa*.  Such interpretations need not be labored further.  They are the primary emphasis of the student but not of this paper.  The concern here has been to focus the attention of teaching ecologists on the possibilities of this type of laboratory exercise as a logical adjunct to serious, mature field analysis.

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# THE ROLE OF THE BISON IN MAINTAINING THE SHORT GRASS PLAINS

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Certain plant ecologists refuse to give the short grass plains the status of a true plant climax, holding that this plant community is a disturbance climax or disclimax brought about by the coming of man and domesticated grazing animals and that the true climax is the mixed grass prairie, which would reappear if pristine conditions were restored. This paper attempts to show that the Great Plains was formerly grazed heavily by bison and other wild animals and that this primitive grazing held the western plains in a short grass stage which cannot be called a disturbance climax because this animal life was natural to the biome.

When in 1876 Charles Goodnight and his vaqueros drove ten thousand buffalo out of the canyon of the Palo Duro in Texas to provide range for jostling hundreds of long-horn cattle he symbolized a movement—the mass appropriation of the feeding grounds of the buffalo for domesticated animals of man. Wild cattle for buffalo, many for many. Goodnight might have called it an even trade so far as the effect on the grass was concerned, but certain plant ecologists would disagree. They say this period marks the beginning of the modification of the mixed prairie by overgrazing of domesticated animals, resulting in what is called the short grass dis-climax (disturbance climax) of the Great Plains (Weaver and Clements, '38, p. 524), the prefix "dis" in this case denoting separation and unlikeness or derogation.

In brief, the text just quoted states (p. 525) that the mixed prairie formerly stretched "from northern Alberta and Saskatchewan through the Staked Plains of Texas and from central North Dakota and Oklahoma on the east to western Wyoming and eastern Utah and southwestward through northern New Mexico and Arizona to the Colorado Valley." The climax was said to be composed of both mid and short grass on more or less equal terms, the major dominants being *Stipa comata, Sporobolus cryptandrus, Agropyron smithii,* and *Koeleria cristata* among the mid grasses and *Bouteloua gracilis* and *Buchloe dactyloides* among the short grasses. Over the drier portion of this area overgrazing by domesticated stock is said to have so handicapped the taller grasses and favored the short grasses that the taller species practically disappeared, leaving an erroneous impression that the short grass plains is a distinct climax of xerophytic nature (p. 524).

To support the position that overgrazing by domestic animals is responsible for the occurrence of the short grass plains three sources of evidence were listed (p. 525) in the text quoted above: (1) the dominance or reappearance of the taller grasses under protection from grazing, (2) rapid reestablishment of the taller grasses in wet years, during which the bad effects of overgrazing are offset by better growing conditions, and (3) photographs of the Hayden Expedition in 1870 which show the domination of the Great Plains by mid grasses.

In the foregoing explanation of the occurrence of the short-grass plains as a disclimax certain difficulties appear that seem to make the position untenable, viz:

(1) the enormous herds of buffalo and other wild animals in former time, (2) the definite statements of early explorers and pioneers that the short grass plains existed there long before Goodnight, Loving, Chisholm, and their kind blazed the cattle trails, and (3) the marked ability of the short grass dominants to withstand heavy overgrazing, which indicates that this environmental factor is not strange or new.

Clements ('36) wrote, "At the outset it was recognized that animals must also be considered members of the climax, and the word biome was proposed for the purpose of laying stress upon the mutual roles of plants and animals." Clements and Shelford ('39, p. 20) stated that "The biome or plant-animal formation is the basic community unit; that is, two separate communities, plant and animal, do not exist in the same area." Weaver and Clements ('38, p. 86) took the position that disclimaxes are almost always the result of disturbance by man or domesticated animals or by the introduction of alien species, and that "man alone can destroy the stability of the climax during the long period of control by its climate" (pp. 80–81). They stated further (p. 478) that animals occupy a position in the climax community similar to that of subdominant plants. It follows then that under the existing definition of biome and disclimax the latter term could not be used to express conditions brought about by normal grazing of wild animals in their pristine numbers. If, as is the purpose of this paper, it can be shown that buffalo and other wild animals kept the drier portions of the plains in short grass, then we have not a short grass disclimax but a short grass climax.

Sufficient information is at hand from various sources to show that the coming of civilized man and domestic animals caused some overgrazing on the plains, but the important point in this case is indicated by the question "Did the buffalo and other wild animals graze intensively enough on the upland plains prior to the coming of white men to give the short grasses wholesale dominance over the taller grasses?" If so, the term "disclimax" gives the wrong concept, for as previously explained a disclimax under existing definition cannot result from the grazing of wild animals in pristine numbers.

Weaver and Clements' statement of the dominance or reappearance of taller grasses in the Great Plains in areas protected from grazing has already been mentioned. Exclosures at the U. S. Northern Great Plains Field Station at Mandan, North Dakota, and relict areas studied by the author in the Badlands of the Pine Ridge Indian Reservation in South Dakota clearly shows this succession, and the experience of Soil Conservation Service range investigators in the Northern Great Plains is in general agreement on this point. However, in portions of eastern Colorado and Wyoming and western Nebraska the dominance of taller grass in protected areas is questioned by some investigators who feel that some local dry-climate parts of the plains are too dry to support mixed grass.

This controversial point need not be further discussed in this paper for the reason that restoration of taller grasses under protection from grazing cannot be used as a source of evidence to support the short grass disclimax point of view. A protected area is not a true sample of the pristine biome. It will be brought out later in this paper that the Great Plains formerly supported millions of wild grazing animals, and therefore any sample areas used for gathering evidence as to the original aspect of the plains must include grazing in the amount originally present in order to give comparable results.

The development of the Relict Method (Clements '34) has meant much to the furtherance of the study of ecology. As Shelford ('31) observed, however, the investigator using this method should always take care to include animals in their early or original numbers, for animal

and plant communities have always been interdependent and intimate in their relations. In recognition of the peculiar significance of buffalo in determining the aspect of the plains he suggested the name Bouteloua—Bison climax. While most plant ecologists have recognized the part of animals in the climax, it seems that in the case of the short grass plains some investigators have apparently failed to appreciate the fact that heavy populations of wild grazing animals would have the same effect on the range as heavy population of domestic animals.

Weaver and Clements offer the reestablishment of the taller grasses in wet years as evidence of the former codominant position of the taller grasses in the short grass plains. However, Russell ('32) and Taylor ('34) point out that it is often the occasional extreme or critical factor that determines the plant composition of a given site, and Taylor's restatement of Liebig's Law of Minimum is worth repeating here: "The growth and functioning of an organism is dependent upon the amount of the essential environmental factor presented to it in minimal quantity during the most critical season of the year or during the most critical year or years of a climatic cycle." With moisture being the common limiting factor to vegetation on the plains it is easy to see how the occasional "desert year" beats back the taller prairie grass species that invade the short grass domain in the more favorable seasons. Reestablishment of the taller grasses in wet years is only the expression of the plus phase of the climatic cycle and, as pointed out above, it is minimal and not maximal quantity that becomes the deciding factor in plant ecesis. Reestablishment of taller grasses in wet years cannot then be used as evidence that the taller grasses are true codominants, because the dry years have more significance in determining the plant composition.

The photographs of the Hayden Expedition are frequently cited as proof that the short grass plains represent a reduction of the mixed prairie due to overgraz-

ing. Comparison of present-day retakes of many of these old scenes with copies of the 1870 originals, reveals that in many of the older pictures the mid grasses were much more in evidence than in the later photos. However, Elliot's articles in Hayden's 1870 and 1871 Reports (1870, p. 445; 1871, p. 275) show that buffalo grass and grama were the only grasses listed of importance west of the 101st meridian, and these accounts check closely with Fremont's. Hayden himself in an earlier report ("U. S. Geological Survey of the Territories for 1867, 1868 and 1869," pp. 77, 110) in summing up conditions in the western half of Nebraska said. "These broad level prairies are covered with a thick growth of short nutritious grasses." "Sheep would thrive well on the short, nutritious grasses." At the same time (pp. 62, 77) he called attention to the tall grass growing in the Platte Valley and the Tekama bottom. There is apparently a discrepancy between the photographic record and the descriptive summary as regards dominance of the mixed prairie grasses. It is well to point out in explaining this discrepancy that in order to show geological formations many of these photographs were taken along streams and valleys where the taller grasses are always more dominant.

There is yet another strong objection to the use of the Hayden photographs to prove the existence of the mixed grass climax. At the time the photographs were taken conditions were singularly favorable for mid grass so far as grazing was concerned. Reports quoted later show that the buffalo-slaughter had been going on for a number of years throughout the buffalo range and that the numbers of these animals had been considerably reduced by 1870. On the other hand, the livestock influx did not gain momentum until several years later. Consequently, the reduced grazing incident to the reduction of buffalo was favorable to the increase of taller grass, and the period 1865–1875 was an interim of undergrazing and was therefore atypical.

Clements ('28, p. 385) offered a "zone of concentration" explanation for the lack of mid grass at the time of settlement of the plains. He said: "The obvious explanation is that while they have been associated in the mixed prairies for thousands of years, the tall grasses were kept down by the buffalo in the zone of concentration resulting from advancing settlement. They reappeared with the going of the buffalo, and the disappearance of the buffalo grasses was nothing more than their being overtopped by bluestems."

This "zone of concentration" explanation does not appear to bear analysis. All source material studied in connection with the preparation of this paper indicates that the buffalo in general were not driven from their range so much as slaughtered upon it. They were stupid animals, pitifully lacking in a sense of danger, and they did not so much retreat in the face of approaching civilization as perish in its path. The buffalo hunter penetrated deep into the heart of the buffalo country far in advance of the settlements, preventing any zone of concentration. References quoted in this paper show that the buffalo population had greatly dwindled by 1870, and Seton ('29) estimated that while by 1870 this population had been reduced to *one-fourth* its pristine number it was occupying somewhat less than *one-third* its former range, which does not indicate a zone of concentration. But the most convincing evidence is the Journal of Lewis and Clark. These men penetrated a vast domain which was unexplored and practically unknown to white men, yet they reported short grass plains to be general throughout the journey across what is now the Dakotas and eastern Montana.

Of the three kinds of evidence listed as supporting the point of view that short grass was the natural climax of the plains under pristine grazing use by wild animals, the first point is the enormous herds of buffalo that are reported by practically all writers of early western life. Definite statements of overgrazing by buffalo are included among the citations quoted in the following paragraphs.

Clements and Shelford ('38, pp. 264 and 273) estimated the number of buffalo in the plains at 30 million and the population in the prairie at 12 million. They estimated the number of antelope in the plains at between 4 and 8 million. Clements ('36) evidently recognized Seton's (Seton '29) estimates of the former population of buffalo and other wild animals but summarily disposed of the possibility of close grazing with a statement that they were distributed over a large area, and the general migratory habits of the animals were such that serious effects from overgrazing or trampling were only local or transitory. He also stated (Clements '35) that the "co-actions of animals grazing are relatively insignificant in nature and rarely become considerable or controlling until man enters the situation." Seton, however, definitely recognized food supply as being the limiting factor in buffalo population and he stated that his estimates were based on the premise that *the plains and prairies were stocked with wild animals as fully as the food supply would permit.* He quoted Col. C. J. Jones as estimating the total number of buffalo on plains and prairies in 1870 at 14 million (Hornaday's estimate was 5½ million). Seton pointed out that bison were at that time occupying less than one-third of their former range and were evidently reduced to one-fourth their former number. He estimated that several hundred years ago when the bison occupied their full range in the interior of this continent they must have numbered 60 million. He estimated the number in the open plains at between 20 and 40 million and the number in the prairies at between 30 and 45 million. We quote excerpts from Seton (1929) as to his method of arriving at the buffalo population of the plains:

"The total area inhabited by the buffalo was about 3,000,000 square miles. Of this area, open plains constituted about one-half. According to figures supplied

me by A. F. Potter, of the Forest Service, the ranges of North and South Dakota, Montana, Wyoming, Nebraska, Kansas, Colorado, Texas, and Oklahoma (a total of about 750,000 square miles, or half of the plains) carried at the time of the last census (1900) about 24,000,000 head of cattle and horses, and about 6,000,000 head of sheep. This means that, when fully stocked, these plains might sustain a number of buffalo at least equal to the number of cattle and horses, but the buffalo had to divide their heritage with numerous herds of mustang, antelope, and wapiti."

"On the other hand, a buffalo could find a living where a range animal would starve. Moreover, many of the richest bottom lands are now fenced in; and we have taken no account of the 6,000,000 sheep. On the whole, it seems that we are safe in placing the number of buffalo formerly living on the entire plains area as about 40,000,000."

"Let us consider the question from another standpoint: There were 1,500,000 square miles of the plains; it takes 30 acres of such range to support an ordinary range beast, which needs as much as, or more than a buffalo. There were as many of the latter as the food could sustain, therefore, the plains had 30,000,-000. But take off one third to allow for the herds of other creatures, and we have 20,000,000 as the number of the plains buffalo."

Seton's estimate of 20 million buffalo on the plains in pristine times was on the basis of 30 acres per head per year. In comparsion, some of the better short-grass ranges cannot at the present time properly support more than this ratio of animals. A buffalo requires about the same amount and kind of feed as a cow, so it is evident that if Seton's estimate of 20 million or Clements' and Shelford's estimate of 30 million buffalo in early days on the plains is anywhere near correct these animals were sufficiently numerous, along with the 4 to 8 million antelope and extensive herds of elk, deer, and

other wild animals, to hold the drier portions of the plains in a short grass stage.

Garretson ('38), present Secretary of the American Bison Society, maintained that Seton's estimate of 60 million buffalo in early days was definitely a conservative figure. He pointed out that before the white man came to this continent the buffalo were extending their range eastward and southward, and this fact alone in the behavior of a game species indicates heavy population or approach to saturation point in the center of population, which was in the Great Plains. He also showed that even as early as 1848 slaughter was well under way. In that year 110,000 robes and 25,000 tongues reached St. Louis from the valley of the Missouri. He called attention to the account of Pedro de Castenada, Coronado's historian, who compared the number of "hump-backed oxen" on the plains to the fishes in the sea and who remarked that the party was never out of sight of buffalo while journeying on the plains.

Hornaday (1889) who made an official report to the U. S. Government on the buffalo extermination shortly after it occurred said of the numbers of these animals: "Of all the quadrupeds that ever lived upon the earth probably no other species has ever marshalled such inuumerable hosts as those of the American bison. . . . To my mind the evidence is conclusive that although the northern herd ranged over such an immense area it was numerically less than half the size of the overwhelming multitude which actually crowded the southern range, and at times so completely consumed the herbage of the plains that detachments of the United States Army found it difficult to find sufficient grass for their mules and horses." Based on information furnished by the famous frontiersman, Colonel Dodge, Hornaday estimated that by 1870 hunting of the buffalo by both whites and Indians had decreased the bison to 4 million south of the Platte and 1½ million north of that river. These estimates should not be regarded as being gross

*variance with stories of vast herds of* buffalo encountered after the railroads were built into the west, for the buffalo —even when decreased in total numbers —often traveled in vast multitudes.

Goodnight, the "Burbank of the range" (Haley, '36), related an incident of starvation of buffalo by the thousands as late as the winter of 1876 near the Brazos River in Texas. He saw dead buffalo so thick "they resembled a pumpkin field" and estimated that shortage of winter feed had killed several million buffalo on a front 100 miles long and 25 miles wide.

Fremont (1845, pp. 144–145) said: "The extraordinary abundance of the buffalo on the east side of the Rocky Mountains and their extraordinary diminution, will be made clearly evident from the following statement: 'At any time between the years 1824 and 1934, a traveller might start from any given point south or north in the Rocky Mountain range, journeying by the most direct route to the Missouri River, and during the whole distance, his road would be always among large herds of buffalo, which would never be out of view until he arrived almost within sight of the abodes of civilization. . . .'"

Colonel Dodge (1876, p. 129) said, "Forty years ago the buffalo ranged from the plains of Texas to beyond the British line; from the Missouri and Upper Mississippi to the eastern slopes of the Rocky Mountains. Every portion of this immense area was either the permanent home of great numbers of buffalo, or might be expected to have each year one or more visits from migratory thousands."

Many other citations could be listed to show that the western plains supported great numbers of buffalo, but those quoted above indicate that a sufficient number of bison existed prior to 1870 to hold drier portions of the plains in a short grass stage. Indeed, the statements of Hornaday and Goodnight show cases of severe and extended overgrazing by wild animals. It is now our purpose to select from the historical record direct statements that

the short grass plains existed prior to the introduction of domesticated animals.

Castenada, the historian of Coronado's expedition to Quivera in 1540, wrote (Winship, 1896): "Who could believe that 1,000 horses and 500 of our cows and more than 5,000 rams and ewes and more than 1,500 friendly Indians in traveling over these plains would leave no more trace where they had passed than if nothing had been there—nothing—so that it was necessary to make piles of bones and cow dung now and then, so that the rear guard could follow the army. The grass never failed to become erect after it had been trodden down and although it was short, it was as fresh and straight as before."

To anyone who has observed the trampling effects of trailing anywhere near the number of horses, cows and sheep mentioned by Castenada, it is very evident that no appreciable amount of taller grass was present in this sward, otherwise the trail would have been very plain. Taller grasses are beaten down and remain that way for some time when trailed over by large numbers of livestock.

Close check of Lewis and Clark's journal (Hosmer, '02) reveals that taller grasses were observed commonly along the early course of the journey up the Missouri before entering the buffalo country. A short distance above the mouth of the Sioux River the first buffalo was seen by the party, and as soon as herds were reported no further mention of stands of taller grasses on the plains was made throughout the journey across the Dakotas and the plains of Montana. The journal recorded (p. 320) that "throughout the high plains and prairies the grass is at no season above three inches in height." Near Marias River in Montana, where vast herds of buffalo were encountered, the party made the following observation (p. 263): "The soil is dark, rich and fertile yet the grass is by no means so luxuriant as might have been expected, for it is short, and scarcely more than sufficient to cover the ground."

Near Great Falls, Montana, with "vast quantities of buffaloes feeding in the plains" the journal (p. 292) observed that the grass was low, "not generally more than three inches high, though it is soft, narrow leafed and affords a fine pasture for the buffaloe."

Fremont (1845) ascended the Republican at the beginning of his second expedition. Until the buffalo range was reached the grasses were reported as being generally "luxuriant and rich." Buffalo grass was not seen until the day before the vanguard of the buffalo herds was met. Once within the buffalo range the "short sward of the buffalo grass prevailed everywhere."

Colonel Dodge (1876, p. 32) said, "The higher portions of the second plain [High Plains] are covered with the famed buffalo grass. It covers the ground very thickly, to the exclusion of the other grasses, or even flowers. The blades are short, but two or three inches long, and curl upon themselves, forming a thick, close mat of beautiful sward.

The noted botanist C. E. Bessey (1887, p. 216) said of the disappearance of buffalo grass in Nebraska: "Already the genuine buffalo grass (*Buchloe dactyloides*) has practically disappeared from the eastern third of the State. Of course I know very well that there are patches of it here and there in these older counties; it may be found in such patches within a mile or two of the capitol building; but these little patches are as nothing when compared with its former extensive distribution. A second grass commonly known by the name of buffalo grass (*Boutcloua oligostachya*) is fast following the first."

"Buffalo grass, *Bulbilis dactyloides*, is widely spread throughout the Sandhill region. This valuable forage plant is rapidly disappearing. Its hard-awned fruits were especially suited for distribution by the buffalo, and since these have disappeared and the prairie fires are no longer allowed to sweep the plains, the buffalo grass is being rapidly choked out by the ranker species" (1893, p. 288).

Wilcox ('11), after compiling the statements of many explorers and travelers with reference to grazing conditions over the prairies and plains during the past century, said: "The present condition of the Great Plains is essentially the same as that described by early travelers. The prevailing grasses are still the buffalo and grama, of low habit. The immense number of buffalo in the early days and later of cattle have not been sufficient to produce any marked change in the character and amount of range forage upon this area."

"These accounts indicate what would naturally be expected, viz., that where buffaloes congregated in immense herds the grass was totally destroyed for the time and the ground was much cut up or packed down, according as dry or wet weather prevailed. The result of such accumulation of large herds was the apparent total destruction of the grass. It should be remembered, however, despite the fact of apparent total destruction wrought by the buffalo along the line of their migration and during their close association at breeding seasons, the range recovered so that the evidence of their destructive grazing was entirely lost within a few years."

The third kind of evidence supporting the position that the short grass plains is not a disclimax is the marked ability of the short grass dominants to withstand heavy overgrazing, which indicates that this environmental factor is not strange or recent. We are told (Fremont, 1845, pp. 143–145) that the buffalo never reached the Pacific states except to penetrate a short way down the Columbia valley. The grasses in the Pacific states had likely experienced lighter grazing under use by deer, elk, antelope, etc., than occurred on the plains to the east of the Rockies, which were crowded with hosts of buffalo in addition to other wild animals. When domesticated animals reached California the perennial by

grasses evidently disappeared under grazing use and fire, leaving only annual grasses to occupy the ground. Clements related (Weaver and Clements, '38, pp. 526–527) that the climax grasses so completely disappeared in this case that for many years ecologists considered the annual grasses to represent the true climax condition and that it was only after painstaking search that sufficient bunch grass relict areas were found to show that the annual grasses were not climax. The plant reaction to domesticated grazing in the Great Plains was in marked contrast to this. None of the characteristic mid grass species completely disappeared from the stand, and the short grasses responded to the new animal components of the biome by an actual increase in dominance so long as grazing did not become too excessive. If the short grasses thrive under moderately heavy grazing today is not that an indication in itself that a similar relationship to the animal world probably existed in pristine times?

In this paper it will be noted that all of the important points brought out in the historical record are carefully corroborated—in some cases several times. Lewis, Clark, Fremont, Hornaday, and Hayden made their reports as official records for the U. S. Government and probably would not have been selected had they not been trusted to make accurate observations. Unfortunately none of our chroniclers were trained botanists, but they could at least distinguish between short and taller grasses which happens to be the important point in this case. Much of the material herein quoted is from daily journals or diaries, or from reports written shortly after an exploration was completed and little of it is in the form of recollections which might have been dimmed or confused from the passage of years.

This paper has attempted to show that buffalo grazing exerted much the same effect upon the plains grassland as grazing by domestic animals has—that overgrazing by domestic animals was matched by overgrazing by buffalo—and that in general the same grass species are dominant today as were dominant in pristine times.

## Summary

Three sources of evidence are offered by Weaver and Clements to support the view that the short grass plains is a disclimax: (1) the dominance or reappearance of the taller grasses under protection from grazing; (2) rapid reestablishment of the taller grasses in wet years during which the bad effects of overgrazing are offset by better growing conditions; (3) photographs of the Hayden Expedition in 1870 which show domination of the Great Plains by mid grasses. An earlier publication by Mr. Clements ('28) offered an explanation that the tall grasses were kept down by the buffalo in the zone of concentration resulting from advancing settlement. This explanation would establish man as a causative factor and would support Mr. Clements' classification.

This paper submits evidence to show that the term "disclimax" gives us the wrong concept of ecological development of the short grass plains and that those plains are a true climax under Clements' definitions of climax, disclimax, and biome. The first point listed above is countered by showing from numerous and reliable quotations from the historical record that pristine buffalo and other grazing animals were almost if not quite as numerous as the later herds of cattle, and that therefore the behavior of areas in the Great Plains under protection from grazing does not give a true picture of biome relationships, and can hardly be accepted as a source of evidence. The second point is met with the objection that reestablishment of the taller grasses in wet years is only the expression of the plus phase of the climatic cycle, and Taylor's restatement of Liebig's Law of Minimum is quoted to bring out the point that minimal quantity, not maximal, is the true determining factor in plant ecesis. The third point meets the objection that

many of the photographs of the Hayden Expedition of 1870 were taken along streams and valleys where geological formations could be shown, and in such locations mid grasses were likely to be dominant even when short grass dominated the neighboring plains. Further objections to this photographic source of evidence are that it disagrees with descriptions of grassland in the narrative summary of the expedition, and that the period 1865–1875 was atypical of range conditions because of reduction of buffalo numbers. The "zone of concentration" explanation is met by showing that in the process of extermination the buffalo concentrated but little if at all at the fringe of civilization and that Lewis and Clark reported vast plains of short grass in areas never before traversed by white men.

Three kinds of evidence are offered by the present writer to support the view that the short grass plains represent the true climax of the pristine biome: (1) numerous and reliable quotations in the historical record show that the former population of wild animals stocked the plains to carrying capacity so that the introduction of domestic livestock after the destruction of wild game was merely a substitution so far as effect of grazing on plants is concerned; (2) direct statements from reliable journals and reports of early explorers and pioneers make specific reference to the existence of the short grass plains long before livestock was introduced; and (3) the marked ability of the short grass dominants to withstand overgrazing, which indicates that this environmental factor is not strange or new.

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# STUDIES IN NOCTURNAL ECOLOGY, IX. FURTHER ANALYSIS OF ACTIVITY OF PANAMA RAIN FOREST ANIMALS [1]

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In a previous paper (Park, '38) a preliminary study of the activity cycles of the Panama rain forest community was reported. The vocalization of typical species was charted and found to have an apparent positive correlation with the periodic fluctuation of the physical influences measured. When such species were placed in recording cages their activity cycle, under relatively normal conditions,

TABLE I

| Animal | General activity |
| --- | --- |
| I. INSECTS | |
| 1. Unidentified orthopterous insect, the "Grillo" of certain of the natives, or "Ting-ting" (?) | Apparently arhythmic, the shrill and metallic note, generally given twice is very elusive and though heard frequently, at any time of the twenty-four hour cycle, is yet unknown. |
| 2. Cicadidae | Generally in late afternoon and dusk but not necessarily so restricted. |
| II. AMPHIBIANS | |
| 3. *Bufo marinus* | Apparently diurnal. |
| 4. *Eleutherodactylus fitzingeri* | Nocturnal. |
| 5. *Eleutherodactylus diastema* | Nocturnal. |
| 6. *Leptodactylus pentadactylus* | Nocturnal. |
| 7. *Centrolene fleischmanni* | Nocturnal. |
| 8. *Hyla phaeota* | Nocturnal. |
| 9. *Engystomops pustulosus* | Nocturnal. |
| III. REPTILES | |
| 10. *Geoamyda annulata* | Diurnal. |
| 11. *Basiliscus basiliscus* | Diurnal. |
| 12. *Anolis frenatus* | Diurnal. |
| 13. *Mabuya mabouya mabouya* | Diurnal. |
| 14. *Thecadactylus rapicaudus* | Nocturnal. |
| 15. *Sphaerodactylus lineolatus* | Diurnal. |
| IV. BIRDS | |
| 16. Cassin's Barred Owl (*Ciccaba virgata virgata*) or Choliba Screech Owl (*Otus choliba luctisonus*) | Nocturnal. |
| 17. Lesser Tinamou (*Crypturus soui panamensis*) | Nocturnal. |
| 18. Greater Tinamou (*Tinamus major castaneiceps*) | Nocturnal. |
| 19. Parrots and Parrakeets (*Psittacidae*) | Diurnal. |
| 20. Toucans (*Rhamphastos piscivorus brevicarinatus* and *Rhamphastos swainsonii*) | Diurnal. |
| 21. Panama House Wren (*Troglodytes musculus inquietus*) | Diurnal. |
| 22. Lawrence's Wood-hewer (*Xiphorhynchus nanus nanus*) | Diurnal. |
| 23. Fruit Crow (*Querula purpurata*) | Diurnal. |
| 24. Panama Blue Grosbeak (*Cyanocompsa cyanoides cyanoides*) | Diurnal. |
| 25. Great Rufous Motmot (*Baryphthengus martii semirufa*) | Diurnal. |
| V. MAMMALS | |
| 26. Black Howler Monkey (*Alouatta palliata inconsonans*) | Arhythmic, but more diurnal than nocturnal. |
| 27. *Marmosa isthmica* | Nocturnal. |
| 28. Numerous Bats, especially *Myotis n. nigricans* | Nocturnal, especially dawn and dusk. |

FIG. 1. Map of Barro Colorado Island, Gatun Lake, Panama Canal Zone, with latitude and longitude, courtesy Mr. James Zetek. Stippled areas represent unmodified rain forest according to Enders (1935).

paralleled the vocalization records in the forest, and followed the twenty-four hour physical environmental rhythm.

In most communities a distinctive nocturnal and diurnal fauna are present, and these are characterized by structural, functional and ecological adjustments to night and day. This larger problem of nocturnalism has been discussed fully elsewhere (Park, '40). The present report continues the analysis of a particular rain forest with respect to the periodism exhibited by its constituent animals. As before, this work was done at the Barro Colorado Biological Station in Gatun Lake during the summer of 1938. At this time both vocalization and recorded activity studies upon animals were resumed, and the following table (table I) lists the majority of the animals observed and their general period of activity.

From investigation of the thirty odd species of animals listed, in conjunction with the data previously reported, there begins to emerge a clear picture of the twenty-four hour periodism in the rain forest, a marked map of which is included at this point (fig. 1). Our data on some of the species are tolerably complete, whereas others are very poorly understood. Information is needed especially on the fireflies, cicadas and ting-ting. With respect to the latter animal, its taxonomic identity is not certainly known. The senior author has spent hours, by day and night, attempting to trace the source of the call described in the table above. This attempt has been made in

FIG. 2. Vocalization of the "ting-ting" near Drayton house during the dusk and dawn of July 9–10, 1938, and the daylight intensity during these two periods in an adjacent clearing; see text for discussion.

company with skilled native woodsmen, alone, with such distinguished herpetologists as Dr. and Mrs. E. R. Dunn, with entomologists and ornithologists, and the call has been ascribed to an insect, a frog or a bird. Native woodsmen insist that it is a form of cricket, but could not produce the animal. The relation of this call to time and light intensity is sketched in table II, and a typical vocalization curve is given in graph form (fig. 2).

From these scattered records it is readily noted that the "ting-ting" calls more frequently at dusk, but calls during the afternoon, through the night and into the early morning hours. Additional data suggest that it calls infrequently through the day and night, so that it appears to be preponderantly nocturnal but not strictly so. The following graph (fig. 2) gives a typical vocalization curve for a population of this animal in the forest near Drayton station.

The large tarantulas (*Eurypelma, Sericopelma*) abounded in the laboratory clearing and their nocturnal habits were observed. It had been previously demonstrated that they were 97 per cent night active when in mechanically recording cages (Park, '38), with the peak of activity coming shortly after dark, between 7:30 and 8:30 P.M. This experimental analysis was checked against observed times of emergence from their burrows and it was found that these large spiders began to appear at the mouths of their burrows between 7:00 and 7:15 P.M. at which time the light intensity varied generally between 0.5 and 0.0 foot-candles at the burrows. The spiders emerged and were active about the burrow entrances from this period on through the night, running into the holes if pursued with a flash-light, only to emerge again, going back to the burrows in the early morning hours as a rule.

TABLE II

| Date 1938 | Time | Light intensity (foot-candles) | Remarks on "Ting-ting" |
|---|---|---|---|
| vii. 2 | 6:57 P.M. | 0.0 in forest 1.5 in clearing | First call since 5:19 P.M. |
| vii. 3 | 6:37 P.M. | 18.0 in forest | First dusk call. |
| vii. 4 | 8:00 A.M. | 1000.0 in clearing | First morning call. |
| vii. 4 | 6:25 P.M. | 77.0 in clearing | First dusk call. |
| vii.19 | 6:02 A.M. | 0.0 in forest | First morning call (air in forest 75 degrees F.) and call given repeatedly to 7 A.M. (the light in forest rising to 4 FC and temperature to 77) both before and during a heavy rain. Called often through afternoon from 3:55 P.M. (light 48 FC) to dusk at 6:36 P.M. (light in forest 0.5 FC). |
| vii.19 | 6:59 P.M. | 0.0 in forest | Last dusk call. |
| vii.31 | 5:35 P.M. | 3.5 in forest | First call since 4:45 P.M. |
| | 6:26 P.M. | 0.0 in forest 10.0 in clearing | Last dusk call. |
| viii. 1 | 6:05 P.M. | 340.0 in clearing | First call since 4:40 P.M. |
| | 6:59 P.M. | 0.5 in clearing | Last dusk call. |
| viii. 4 | 10:15 P.M. to | 0.0 | Calling repeatedly through the night, as often as |
| viii. 5 | 12:14 A.M. | 0.0 | ten times per minute. |
| viii. 5 | 6:07 P.M. | 190.0 in clearing | First dusk call. |
| | 6:32 P.M. | 27.0 in clearing | Last dusk call. |
| | 10:00 P.M. to | 0.0 | Calling repeatedly through the night. |
| | 11:49 P.M. | 0.0 | |
| viii. 6 | 3:04 P.M. to 3:09 P.M. | | Calling in forest. |
| viii. 8 | 5:44 A.M. | 0.0 in clearing | First morning call. |
| | 6:09 A.M. | 12.0 in clearing | Last morning call. |
| viii.11 | 5:58 A.M. | 1.4 in clearing 0.0 in forest | First morning call. |
| | 6:05 A.M. | 8.0 in clearing 0.0 in forest | Last morning call. |

A number of the animals listed in the first table, for example the Black Howler monkeys and the reptiles and amphibians in part, were previously reported upon. Some of these animals, however, deserve special consideration and their general dawn and dusk vocalization is presented in graphic form in the following figure (fig. 3). In this figure one minute of activity is represented by one small space on the circular clock graph, and it should be understood that the day and night proper are not given, only dawn (5:45–7:00 A.M.) and dusk (4:30–7:00 P.M.). These are the two periods of the twenty-four hours when the diurnal and nocturnal species are mutually intermingled in a falling and rising curve of activity, and such periods are especially notable in the tropics. The average course of intensity of daylight in the clearings is presented in figure 4, as well as the intensity of daylight in the forest and

should be consulted in connection with the vocalization record of figure 3, since light intensity is intimately associated with other periodic changes in the physical environment such as temperature, humidity and evaporation. The general course of air temperature and relative humidity in the clearings is given in figure 5 and these same influences are presented for the forest in figure 6. A comparison of these last two figures brings out sharply the much greater constancy of the forest habitat as contrasted with the open spaces, and indirectly demonstrates the great effect of the rain forest canopy and lower strata of vegetation upon the physical environment of the forest animals. This is reinforced by study of the light intensity curves in the clearing as compared with that of the forest floor. With such a characteristic flattening of the light, temperature and humidity curves, the great periodicity of the forest animals is

the more remarkable. One wonders especially concerning the releasing stimulus for those nocturnal and diurnal species which inhabit burrows in the floor, or pass their quiescent phase beneath bark or in other darkened habitat niches. Here the physical environmental changes must be slight indeed. It is possible that some

of the animal constituents have an inherent activity pattern, and that in other species the activity pattern is habitual but slightly strengthened by small changes in the physical environment. It is also possible that a third group of species does not respond directly to the physical environmental periodism, but their releasing stim-
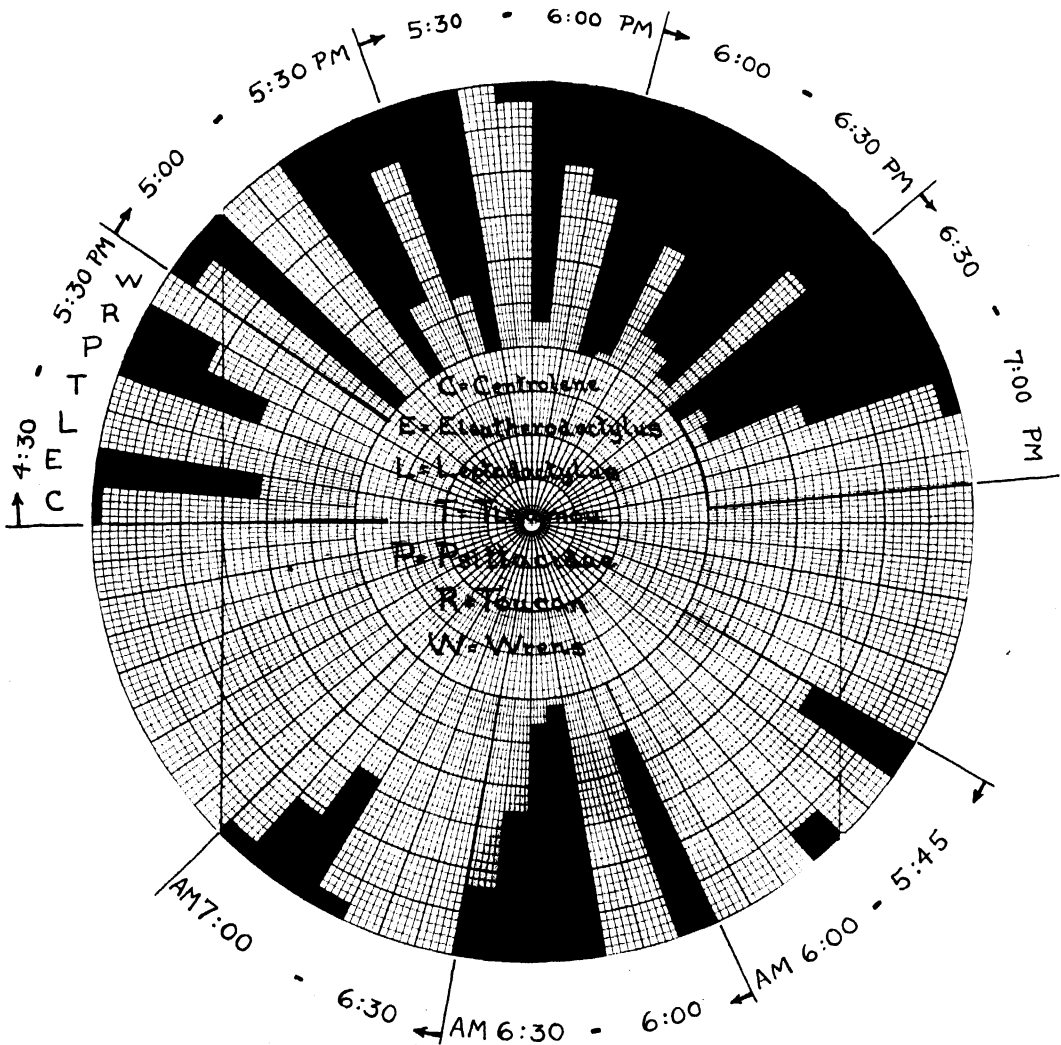


Fig. 3. Vocalization clock-diagram of six representative rain forest species or groups of related species, and the Panama House Wren. The first four are generally nocturnal, the last three generally diurnal: C, *Centrolene fleischmanni;* E, *Eleutherodactylus fitzingeri;* L, *Leptodactylus pentadactylus;* T, Lesser and Greater Tinamou; P, Psittacidae; R, Toucans, Rhamphastos; W, Wren, *Troglodytes inquietus.* Two periods are represented, dusk and dawn. Dusk is divided into five thirty minute periods, each with seven radial columns, one for each animal listed and dawn in two thirty minute and one fifteen minute period, each with seven radial columns. Each column represents the time interval of a given period, one calibration standing for one minute. For example, the frog, Centrolene, is vocalizing for thirteen minutes between 5:45–6:00 A.M. and thirty minutes between 6:30–7:00 P.M. These vocalizations are averages for July and August, 1938. Compare these data with figure 4.
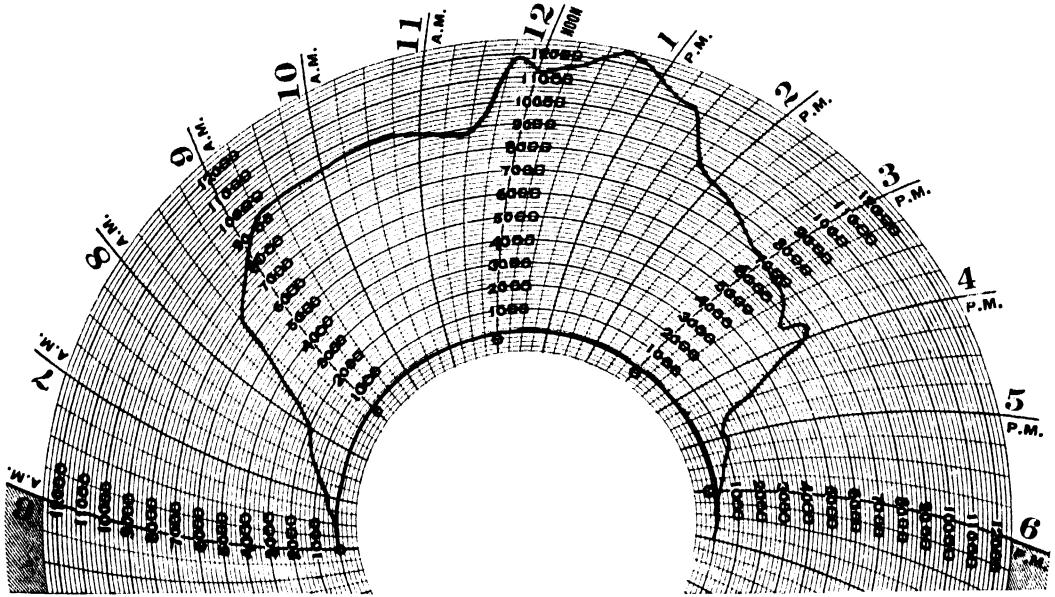
Fig. 4. Average daily march of daylight intensity for July and August, 1938 at Barro Colorado Island, for the open clearing where it reaches an average of ten to more than twelve thousand foot-candles near the middle of the day, and for the rain forest floor where the light seldom exceeds one hundred foot-candles. Data taken with a Weston illuminometer equipped with quartz plates, the sensitive plates being held parallel with the ground stratum for all readings. (No readings taken in the rain, so that average curve represents relatively bright sky rather than true average.) Compare with figures 5 and 6.

ulus is a biological one, for example the onset of hunger or the vocalization of animals in the other groups. Finally, there is the possibility that other animals respond directly to slight changes in the physical environment.

Much careful experimentation must be done under controlled conditions, and under normal fluctuating conditions, before the nocturnal and diurnal animals can be more thoroughly understood. In the mean time these four possibilities remain. There is undoubtedly a composite and complex web of activity patterns involved which challenges investigation. Some field data are available that indicate that the cicadas emit their sounds due to moderately complex stimuli. Thus, when cicadas are studied through the late afternoon and into the night, it appears that they "sing" in groups or aggregations. The interval between bursts of song is longer in the early part of the period noted, and as dusk ensues the interval becomes shorter and shorter. Secondly,

these aggregations, often the population of one or of several adjacent trees, start singing suddenly and stop more gradually: quite often one can detect a "leader"; that is, a cicada that begins singing just perceptibly in advance of the group. This singing in the late part of the day is negatively correlated with the rapid decline in light intensity. Whether this is an apparent or a real correlation must be demonstrated experimentally; that is, temperature or some other influence may be directly involved. At any rate, as the light declines in intensity, the singing increases. But this group singing increases both in intensity and in the number of animals involved. For example, if one measures the light intensity in a clearing, but near the forest margin, the group song of a cicada population can be heard in the forest long before the light is gone in the clearing; as the light drops still further, a second cicada aggregation begins singing much nearer to the clearing, and when the light is so low in the clearing
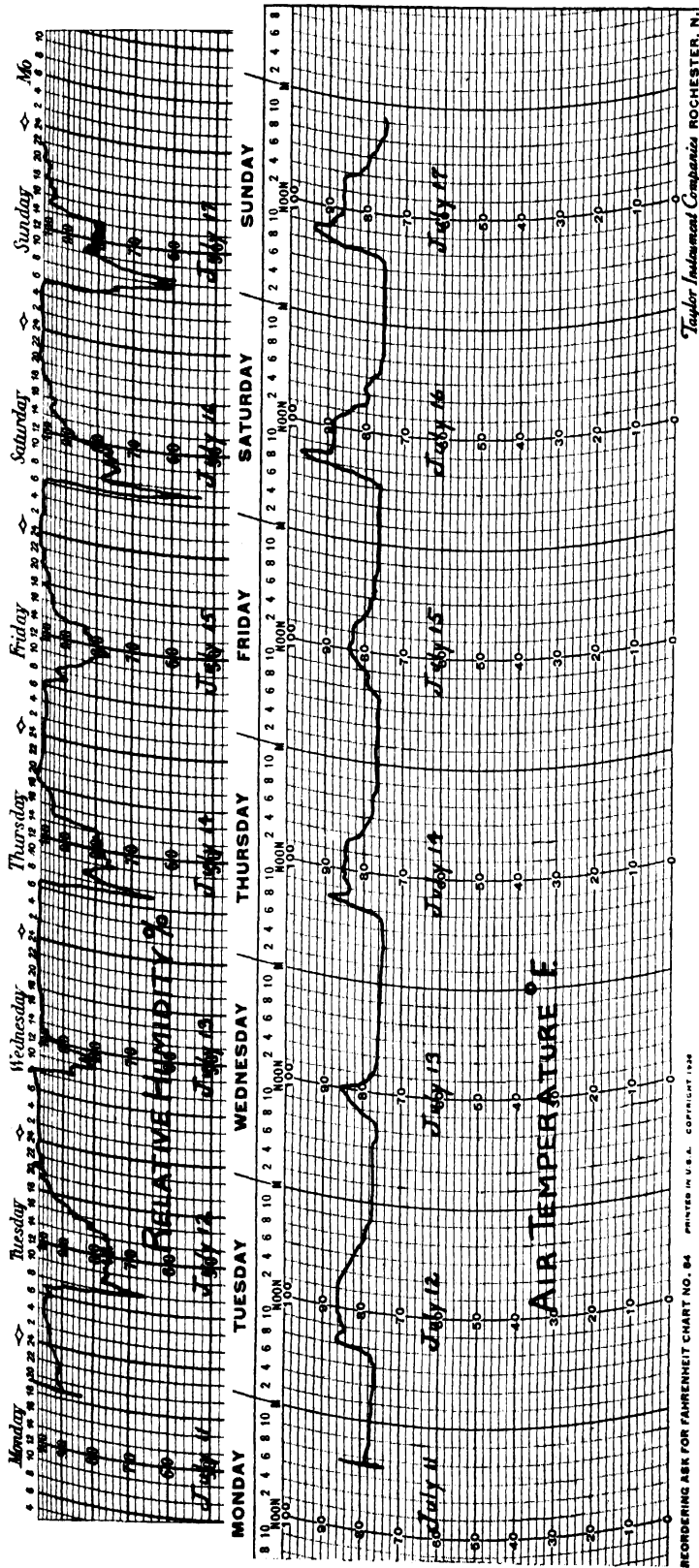
FIG. 5. Typical cycle of air temperature (bottom line) and relative humidity (top line) in the clearings at Barro Colorado Island between July 11–17, 1938. The air temperature by Taylor recording thermograph, the relative humidity by Lambrecht recording instrument. Both instruments checked every other day against battery of nitrogen-filled mercury thermometers and certified sling psychrometer respectively.
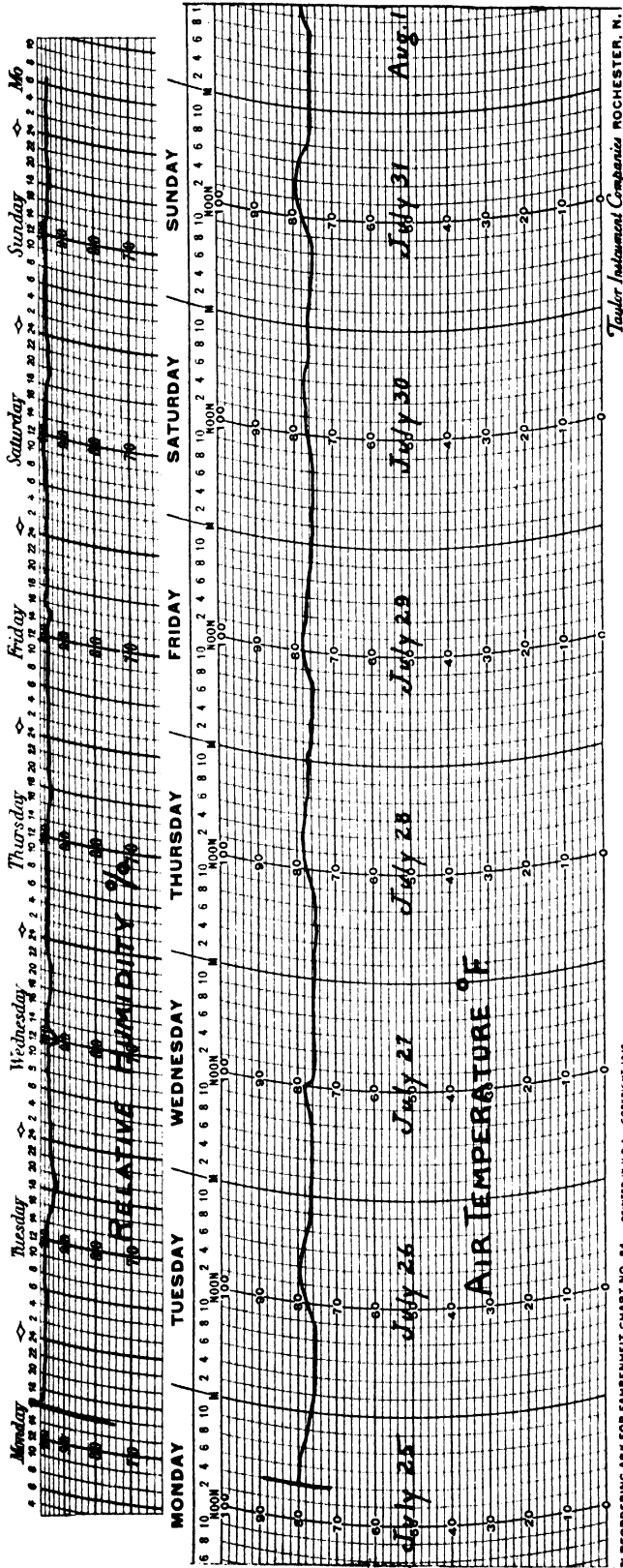
FIG. 6. Typical cycle of air temperature (bottom line) and relative humidity (top line) in the rain forest at Barro Colorado Island between July 25–August 1, 1938. Same instruments as in figure 5. Note typical flat records.

that the illuminometer can just be read, a third aggregation of cicadas begins sound emission, so that the singing of the insects comes in waves, each group more or less keeping its own tempo. In such a case is some slight change in the physical environment responsible for stimulating the first population deep in the forest? Are subsequent cicada groups stimulated independently by the same change at a later time nearer the clearing, or are they biologically stimulated by the sound emission of the first group? Obviously, here is a complex problem, involving a study of the ability of cicadas to receive and react to cicada sound emission, as well as the relation of population to population, leadership of the group sound emission, differential response to light intensity, temperature, relative humidity et al. The following graphs (fig. 7) point out, but do not explain this situation.

These and innumerable special activity problems are more or less covered by the dramatic burst of activity, especially as vocalizations, of the total nocturnal and
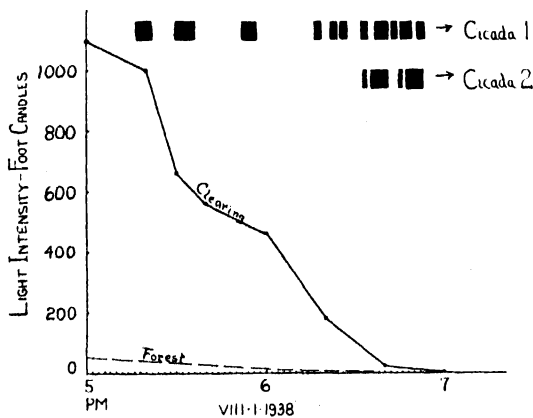


Fig. 7. Apparent correlation between "group singing" of cicadas and light intensity. Cicada 1 represents a population of cicadas deeper in the forest than Cicada 2, which is a population of cicadas much nearer the forest margin. Note that sound emission tends to come in bursts, with shorter intervals as the light intensity decreases. Cicada population sound emission is represented by one small square being equivalent to one minute of sound and the two light intensity curves are plotted in foöt-candles for the same evening, in the open clearing and in the forest.

diurnal fauna at dusk and dawn. A number of these species have been separated on the basis of their vocalization (fig. 3), and the total vocalization is shown, together with the light intensity, for dawn (fig. 8) and dusk (fig. 9). At both of these periods it will be seen that the volume of sound begins, swells, and diminishes within the space of two hours. In both of these figures of total vocalization one small square represents activity of an individual, or aggregation of individuals, for one minute.
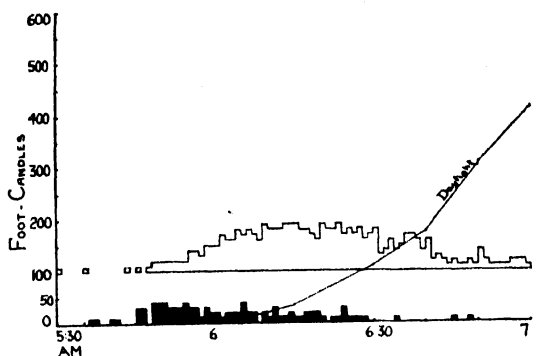


Fig. 8. Average vocalization for all species studied at Barro Colorado Island in summer of 1938, for the dawn period. Light intensity in foot-candles is the average for dawns studied. White block shows sound emission of diurnal, while black block shows sound emission for nocturnal, animals. One small square represents sound emission for one species, or group of closely allied species (table I), for one minute.

The activity of some animals is not so gradual in its intensity. Thus the very large amphibian *Leptodactylus pentadactylus*, which passes the day in deep burrows in the forest floor, emerges and begins vocalizing usually between 6:30–6:35 P.M. (fig. 10) when the light intensity in clearings is falling rapidly between 100 and 50 foot-candles, and the light intensity of the forest floor is between 5 and 0.5 foot-candles. This average sudden vocalization increase checks perfectly with the sudden rise in vocalization of this species reported previously (Park, '38), and contrasts with the gradual rise in vocalization of such
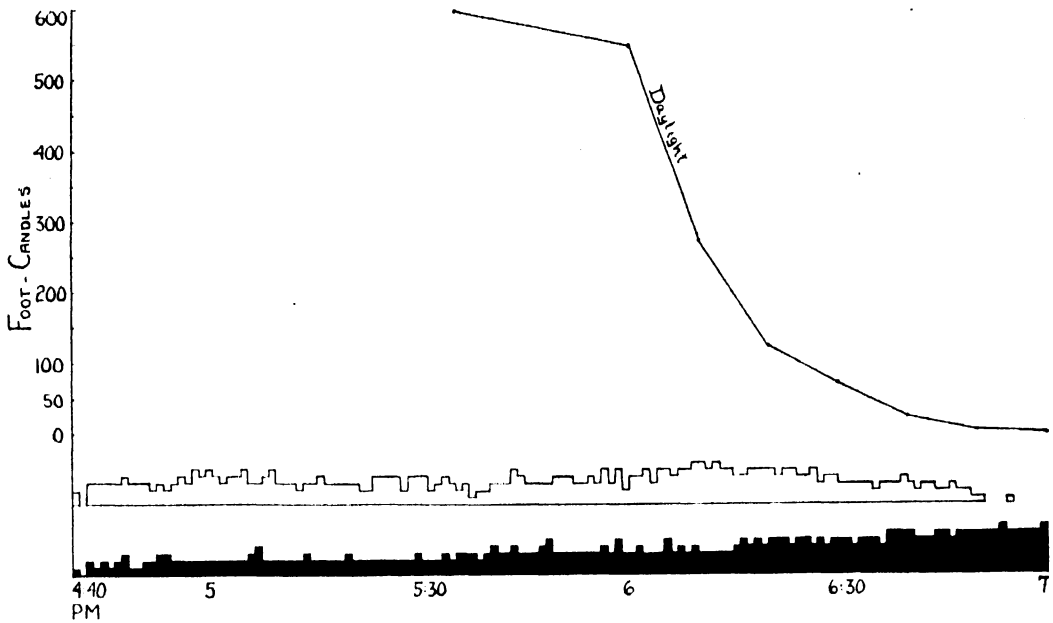
FIG. 9. Average vocalization for all species studied at Barro Colorado Island in summer of 1938, for the dusk period. See figure 8 for explanation.
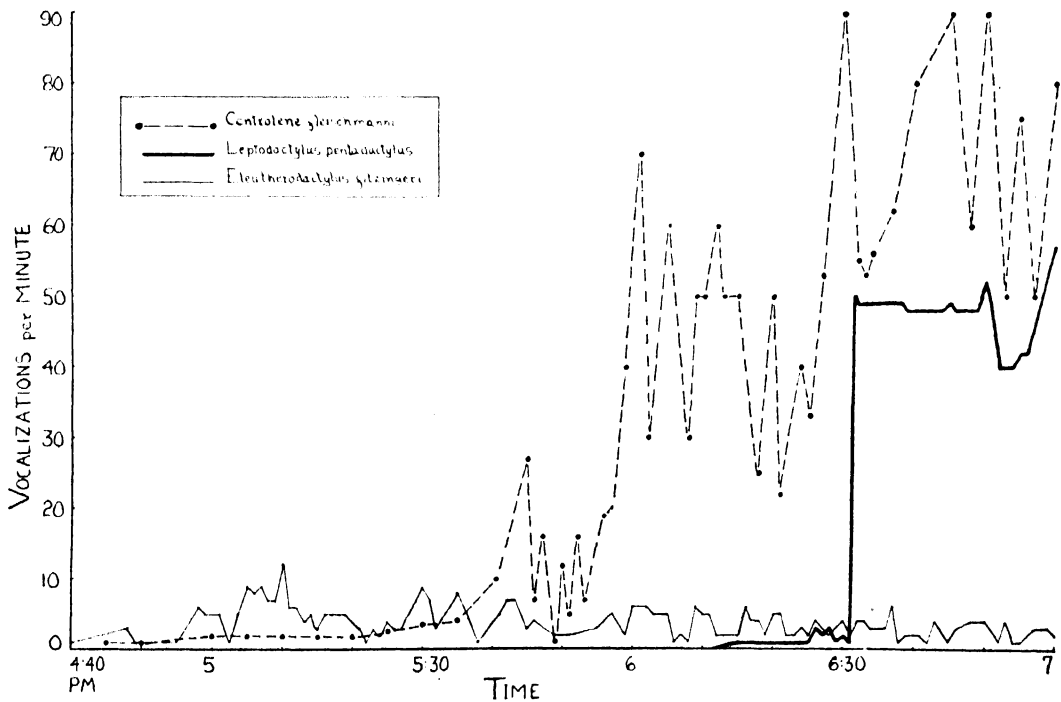
FIG. 10. Average vocalization for three types of sound emission: 1. The small frog, *Eleutherodactylus fitzingeri*, nocturnal, with nightly sound begun and maintained in intensity; 2. The small frog, *Centrolene fleischmanni*, nocturnal, with nightly sound begun and gradually built up by the local population to a relatively high intensity of over ninety chirps per minute; 3. The large frog, *Leptodactylus pentadactylus*, nocturnal, as a representative of the eruptive type, with sound begun and suddenly increased to a relatively stable intensity.

animals as the Tinamou, *Eleutherodac-tylus fitzingeri, Centrolene fleischmanni* and others.

In addition to these data, a number of species was studied by means of mechanically recording apparatus. The equipment was simple, the movements of the specimen being translated via springs to a tambour leaving a record on a twenty-four hour drum, as figured and described in an earlier paper (Park, '38). Of the animals used, three deserve mention at this time.

The giant toad, *Bufo marinus,* was the most surprising of the animals used. Individuals were repeatedly captured on or near the trails during the day, and when this species was placed in the recording cages its preponderant activity was diurnal. Some records showed a secondary rise in activity in the evening between five and seven, but no individuals were active through the night although sustained activity through the day was obtained with some individuals. This apparent diurnalism should be investigated since it is contrary to the general nocturnalism of frogs and toads (Park, '40), and quite counter to the deeply seated activity pattern of our northern *Bufo americanus* and *Bufo fowleri* (Higginbotham, '39), as well as to the activity periodism of other frogs and toads in the rain forest (Park, '38 and data presented here). On the other hand our data on this species are too few to more than draw attention to its activity; it is quite possible that extended investigation may find this toad more nocturnal than our few records would indicate.

Reliable information was obtained upon two other forest species, the floor inhabiting turtle, *Geoamyda annulata,* and the small marsupial, *Marmosa isthmica.* Both field observations and recording equipment showed that the turtle was diurnal, while the marsupial was nocturnal. In both cases the species were hardy enough to survive the boat trip back to the United States, and the turtles have been kept in the laboratory for a

year, feeding upon fruit and vegetables, laying eggs and allowing their activity pattern to be checked under laboratory conditions. The small marmosas are wholly and notably nocturnal. They can be seen in the forest at night, sitting on a branch or hanging from the latter by their prehensile tail, holding a small fruit and feeding, their eyes shining red in the torch-light. In captivity they fed on plantain and a large variety of orthopterous insects. The species has been studied by many, and these life history notes collated and added to by Enders ('35) so that our remarks will be limited to the activity cycle of the species. Their activity was recorded under the normal fluctuation of the physical environment, so that no conclusion can be reached at this time concerning the nature of the pattern. They are quite inactive during the day, remaining curled up and usually asleep until dusk. Between six and seven o'clock in the evening the marmosa becomes suddenly active, the rapid rise in activity resembling in this respect the pattern of the amphibian *Leptodactylus pentadactylus* and the tarantulas (*Eurypelma* and *Sericopelma*). This activity remains nearly maximal through the night and decreases in the early morning hours, ceasing usually before seven in the morning. The nature of the pattern, under the conditions used, was a stable one and not appreciably distorted by the time spent in captivity, nor by the time at which the experiment was started. The average activity cycle is charted for these two species in figure 11, and the following table (table III) gives five typical trials for the marmosa.

The thorough nocturnalism of the marmosa is clear from a comparison of the above figures, even under the artificial conditions of the recording equipment. The number of hours at night when the animal is in continual activity seems too high and possibly represents the normal level of activity plus an additional increase in activity per hour as a consequence of the stimulation of the artificial
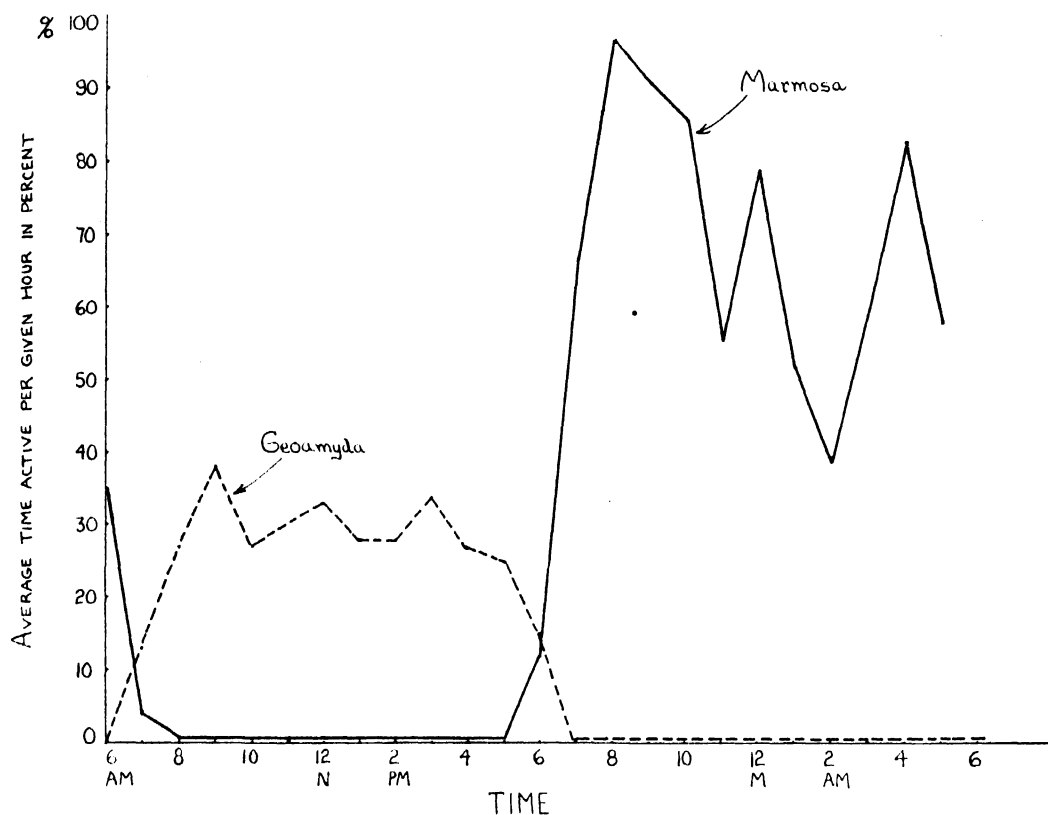
FIG. 11. Average activity of two rain forest species. Data obtained with mechanical recording apparatus and represent bodily movements, not sound. Solid line represents the wholly nocturnal marsupial, *Marmosa isthmica;* broken line represents the turtle, *Geoamyda annulata.* In both species, activity units per hour have been cast into percentage of time active per given hour for purposes of comparison. Curves represent averages for all trials.

TABLE III. *Activity of Marmosa isthmica*

| Date | Start | Percentage of time active for a given hour | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 6–7 A.M. | 7–8 | 8–9 | 9–10 | 10–11 | 11–12 Noon | 12–1 P.M. | 1–2 | 2–3 | 3–4 | 4–5 | 5–6 |
| vii.20 | 7 P.M. | 12% | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| vii.22 | 9 A.M. | 36% | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 |
| vii.31 | 9 A.M. | 50% | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| viii. 2 | 1 P.M. | 0% | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| viii. 6 | 11 P.M. | 25% | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 |
| | | 6–7 P.M. | 7–8 | 8–9 | 9–10 | 10–11 | 11–12 Mid't | 12–1 A.M. | 1–2 | 2–3 | 3–4 | 4–5 | 5–6 |
| vii.20 | | 0% | 62 | 100 | 100 | 100 | 50 | 75 | 100 | 12 | 0 | 12 | 100 |
| vii.22 | | 0% | 75 | 100 | 100 | 75 | 12 | 100 | 36 | 15 | 75 | 0 | 50 |
| vii.31 | | 0% | 25 | 100 | 100 | 75 | 100 | 75 | 0 | 12 | 100 | 12 | 0 |
| viii. 2 | | 50% | 100 | 100 | 100 | 100 | 100 | 75 | 0 | 0 | 12 | 100 | 0 |
| viii. 6 | | 25% | 90 | 100 | 75 | 100 | 75 | 75 | 75 | 75 | 75 | 75 | 100 |

nature of the recording cage. In any case, whether the normal level is 75 per cent or 100 per cent for a given hour, the nocturnalism is evident and this fact is the only one which may be drawn from these preliminary experiments. The rôle of environmental stimulation, habit, inherent periodism, hunger, age and, in the female, of reproductive cycles, remains to be ascertained.    .

## SUMMARY

This is the second of two descriptive papers upon the twenty-four hour activity cycle in a particular rain forest, on Barro Colorado Island, in Gatun Lake, Panama Canal Zone. The daily march of such periodic physical influences as light intensity, air temperature and relative humidity is measured both in the forest and in clearings, and these operating factors appear to be correlated with the activity of the rain forest community, both for the diurnal and for the nocturnal constituents, and for species resident in

the subterranean, floor and higher strata. This periodism is especially well shown at dawn and dusk; for a wide variety of animals including spiders, hemipterans, amphibians, reptiles, birds and mammals. The species activity patterns, although specific, may be studied directly by vocalization in the field, or indirectly by recording apparatus in the laboratory and both types of data are presented in this report.

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# THE NATURAL ESTABLISHMENT OF PINE IN ABANDONED FIELDS IN THE PIEDMONT PLATEAU REGION

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## INTRODUCTION

Abandonment of fields from cultivation is a common occurrence in the Piedmont region of the southeastern seaboard states, particularly in the cotton belt where the soil depleting methods associated with tenant farming on a cash crop basis are most widely practiced. There may be various contributory causes, but basic reasons for abandonment are erosion and physical deterioration of the soil to a point where it is no longer profitably productive.

Practically all abandoned land in the Piedmont sooner or later reverts to pine as the first arborescent stage in the plant succession. Loblolly pine (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Mill.) are the most important species. In the upper Piedmont near the mountains, particularly northward, Virginia pine (*P. virginiana* Mill.) is common, and loblolly rare or absent. On some fields, pines become established promptly after abandonment in densities high enough for satisfactory timber production. Frequently, however, the invasion of pines is spotty and erratic, and the resultant stands are of poor quality because of understocking during the first 20 or more years.

The present study was made in the summer of 1937 to ascertain and evaluate the factors which influence or control the establishment of pine in old fields of the Piedmont Plateau in the Carolinas and southern Virginia. Interest was centered particularly on: (1) the importance of differences in quality of seed source as expressed by the reproductive capacity of parent stands, including such related factors as distribution of seed trees about a field, and their direction from it; (2) relation between distance from seed source and density of reproduction; (3) effect of differences in habitat resulting from topographic factors, soil, and plant cover; (4) time required for establishment of pine; (5) comparison of the important native species of pine; and (6) successional relations.

## METHODS

The study was based on analyses of examples of natural stocking to pine, rather than on experimentation, because only one field season could be spent on the work, and also because at least tentative results were in immediate demand. Fields undergoing invasion by pine were located by random search from the public roads, and examples selected which met the following specifications:

(1) Proximity to a parent stand which had remained in approximately the condition existing at the time of abandonment.

(2) Sufficient size to display a gradient of density of stocking, *i.e.*, the effects of distance from seed trees. Ordinarily, 5 chains (330 ft.) was the minimum distance acceptable.

(3) Freedom from serious disturbances, such as pasturing, burning, or cutting.

(4) Period of abandonment of less than 12 years.

Fields conforming to these specifications were examined in accordance with the following:

(1) Quality of seed source.

(2) Location of seed source with respect to the field.

(3) Density of stocking over the field.

(4) Character of the herbaceous vegetation.

(5) Character of the site, particularly its soil conditions.

(6) History of the field.

Seed sources were classified by quality grade as follows:

*Class 1, good to excellent seed source.*
Stands 40 or more years old and 50 per
cent to fully stocked, in which the indi-
vidual trees, or at least those at the edge
of the stand near the field, were charac-
terized by vigorous growth, well devel-
oped crowns, and abundant cone produc-
tion.

*Class 2, fair seed source.* Intermediate
between classes 1 and 3.

*Class 3, poor or inadequate seed source.*
Included (1) stands less than 40 years
old, (2) stands markedly understocked,
or situations where no actual stand but
only a few isolated trees bordered a field,
(3) stands greatly overstocked and stag-
nating, (4) stands making poor growth
because of low quality of site. Low seed-
producing capacity in (3) and (4) above
usually was indicated by poor crown
form, unthrifty growth, and paucity of
cones on the branches.

Data on the density and distribution of
reproduction were taken by plots .004
acre in size (13.2 feet square), spaced at
1-chain or one-half chain intervals along
lines running from the seed source to
the far side of the field. Usually 2 to 6
such lines, parallel to each other and 2
chains apart, were run on each field.

Pine seedlings were tallied for each plot
by species and 1-foot height classes. As
the lines were run, an outline map of each
field was sketched, and on it were shown
the position of each line and plot, position
of the parent stand or individual seed
trees, and major topographic features.
Important herbaceous species with esti-
mates of their abundance were recorded
for 10 plots mechanically selected from
the line tally plots on each field. Site de-
scriptions included general notations on
topographic position, slope, aspect, amount
of erosion, and identification of soil type.
Period since abandonment and other his-
torical data were obtained as far as prac-
ticable by local inquiries, and by interpre-
tation of such evidence as remains of
crop plants, type of herbaceous cover, and
age of oldest tree seedlings.

In all, 43 fields were intensively exam-
ined, of which 28 were in South Carolina,
13 in North Carolina and 2 in Virginia.
These can be grouped with respect to time
since abandonment into the following
classes: in the first year of abandonment,
4 fields; abandoned 1–3 years, 11 fields;
4–6 years, 9 fields; 7–9 years, 8 fields;
10 or more years, 11 fields. By classes of
seed source they are grouped as follows:



FIG. 1. ᐧ Natural establishment of a young mixed stand of loblolly pine and shortleaf pine in
an abandoned field in the lower Virginia Piedmont. Densities of stocking such as this appear
only in proximity to prolific sources of seed such as are shown in the right background.

class 1, 22 fields; class 2, 16 fields; class 3, 5 fields. These proportions of fields in the different seed source classes do not indicate true proportions in the region; actually, first class seed sources are in the minority. After examining a few fields with poor seed sources, it was not considered worth-while to continue intensive studies where poor stocking obviously was a result of inadequate seed supply.

## IMPORTANCE OF FACTORS INFLUENCING SEEDLING ESTABLISHMENT

It became increasingly evident as the study progressed that the widespread failure of abandoned fields to become satisfactorily stocked to pine could be attributed mostly to the scarcity of seed trees, resulting from intensive and repeated cutting of merchantable timber; furthermore, that seed supply, as determined by quality of seed source and distance from seed source, is the paramount factor controlling density of pine invasion. The effects of site, soil and plant cover, within rather wide limits, seem usually to be important only in their extreme manifestations. As regards direction of seed source in relation to prevailing winds, the data were found inadequate to justify any generalization except that this factor, too, seems to be of comparatively minor importance.

### Quality of seed source

The importance of a prolific source of seed as the most direct and indispensable requirement for satisfactorily dense invasion of pine into abandoned areas is well illustrated by the records of the intensively studied fields. At any given distance from seed source, the average density in seedlings per acre decreases markedly as quality of seed source declines. For example, at the distance represented by the average 5-chain point on the lines of plots, the densities for all fields studied (excepting a few small ones and those complicated by multiple seed sources) which had been abandoned 4 or more years were as follows: class 1 seed

source (average of 8 fields), 948 seedlings per acre; class 2 seed source (average of 10 fields), 482 seedlings per acre; class 3 seed source (average of 5 fields), 150 seedlings per acre. Converted to percentages, the figures for seed source classes 1, 2, and 3 are 100, 51 and 16 per cent, respectively.

The effectiveness of a seed source is of course influenced by its distribution in relation to the area supplied. As a general rule, a parent stand must extend along practically one entire side of a field in order to assure adequate dissemination of seed over it. Effectiveness of seed source is further enhanced when seed trees grow along more than one side of the field. This is most apparent where seed trees are present along two connecting sides. The density of seedlings practically always is greater in a corner thus bounded than in any other part of the field.

### Distance from seed source

Assuming the presence of an adequate source of seed, it is necessary to know how far such seed source is effective.
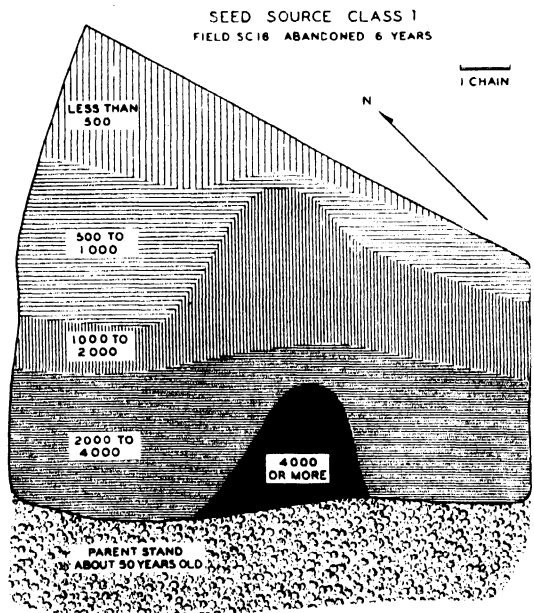


FIG. 2. Map of a field adjacent to a class 1 seed source, showing zones of seedling density. The numbers indicate seedlings per acre.

TABLE I. *Distances from seed source to which different densities of seedlings had become established, and certain descriptive data, for 15 fields exemplifying comparatively good stocking*

| Field Number | Class of seed source | Distances in chains, for different densities expressed as seedlings per acre | | | Soil type | Severity of erosion | Type of plant cover | Species of pine |
|---|---|---|---|---|---|---|---|---|
| | | 2000 or more | 1000 or more | 500 or more | | | | |
| *Fields abandoned 1–3 years* | | | | | | | | |
| SC-8 | 1 | 2.0 | 4.0 | 6.0 | Alamance stony silt loam | Moderate | Broom sedge-goldenrod | Loblolly |
| SC-11 | 1 | 3.0 | 5.5 | 7.0 | Davidson clay | Moderate to severe | Broom sedge-goldenrod | Loblolly; some shortleaf |
| SC-28 | 1 | 2.0 | 3.5 | 4.5 | Cecil sandy loam | Moderate | Aster-trumpet creeper-annual weeds | Loblolly; some shortleaf |
| NC-4 | 2 | 0.0 | 1.5 | 2.0 | Appling sandy loam | Moderate to severe; gullied | Broom sedge-bracted plantain | Shortleaf |
| Average | 1 | 2.3 | 4.3 | 5.8 | | | | |
| *Fields abandoned 4–12 years* | | | | | | | | |
| SC-9 | 1 | 0.0 | 6.0 | 7.0 | Herndon-Alamance silt loam | Slight to moderate | Broom sedge | Loblolly and shortleaf |
| SC-16 | 1 | 3.5 | 6.0 | 7.5 | Herndon stony silt loam | Moderate to severe | Broom sedge | Loblolly |
| SC-21 | 1 | 5.0 | 7.5 | 10.0 | Wilkes sandy loam | Moderate to severe; gullied | Broom sedge-button weed-trumpet creeper | Loblolly |
| SC-24 | 1 | 2.0 | 3.5 | 4.5 | Appling clay loam | Severe (sheet) | Bracted plantain-buttonweed | Loblolly; some shortleaf |
| NC-3 | 1 | 1.5 | 3.0 | 3.5 | Appling sandy loam | Moderate | Broom sedge-goldenrod | Shortleaf |
| NC-13 | 1 | 3.0 | 4.5 | 7.5 | Cecil sandy loam | Moderate | Broom sedge-stone clover | Loblolly and shortleaf |
| Va-1 | 1 | 3.0 | 3.5 | 5.0 | Iredell loam | Moderate | Broom sedge-thoroughwort | Shortleaf |
| Va-2 | 1 | 2.5 | 4.5 | 6.0 | Louisa sandy loam | Moderate to severe | Broom sedge-goldenrod | Loblolly and shortleaf |
| SC-4 | 2 | 2.5 | 3.0 | 5.0 | Iredell loam | Slight | Broom sedge-trumpet creeper | Loblolly |
| SC-6 | 2 | 2.5 | 3.5 | 4.5 | Iredell loam | Slight | Broom sedge | Loblolly |
| NC-9 | 2 | 1.5 | 2.0 | 4.0 | Iredell-Herndon silt loam | Moderate | Broom sedge-poverty grass | Shortleaf |
| Average | 1 | 2.6 | 4.8 | 6.4 | | | | |

SEED SOURCE    CLASS 2
FIELD SC 6   ABANDONED 12 YEARS AGO
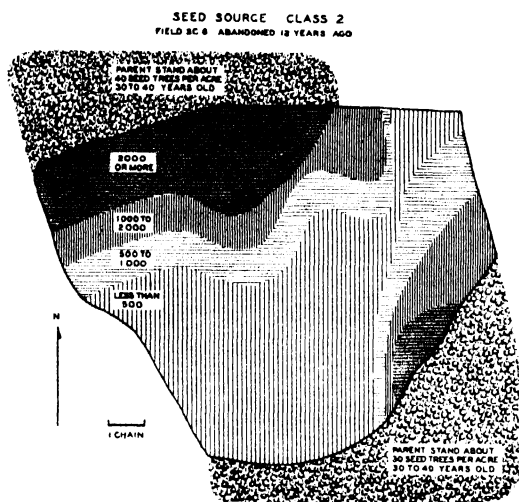


Fig. 3.   Map of a field adjacent to a class 2 seed source, showing zones of seedling density. Although this represents comparatively good stocking for class 2 seed sources, note that the widths of the higher density zones are considerably less than in fig. 2.

Although it is not unusual to find scattered seedlings at distances of one-fourth mile or more from seed trees, the pertinent question is the distance to which

seeds are dispersed in sufficient quantity to produce a satisfactory density of stocking. It is in this connection that the plot tallies are most informative.

Because of irregularities in the shapes of fields and in distribution of seed trees, distances measured along the plot lines often were not true measures of distances from the nearest source of seed. To get a closer estimate of actual distances, isodensity lines delimiting zones of different seedling densities (figs. 2 and 3) were drawn on the maps of 15 fields selected as representing comparatively good stocking. Some smoothing of the isodensity lines was effected by basing them on 3-plot running averages rather than on individual plot counts. These maps were very helpful in depicting distribution of seedlings in relation to position of seed source, particularly when two separate stands had contributed seed to the same field (fig. 3), and greatly facilitated determination of the average distances from seed source to which different densities of stocking had become established. Table I shows the average distances for densities of 2,-



FIELDS WITH CLASS 1 SEED SOURCES
FIELDS WITH CLASS 2 SEED SOURCES
AVERAGE FOR CLASS 1 SEED SOURCES
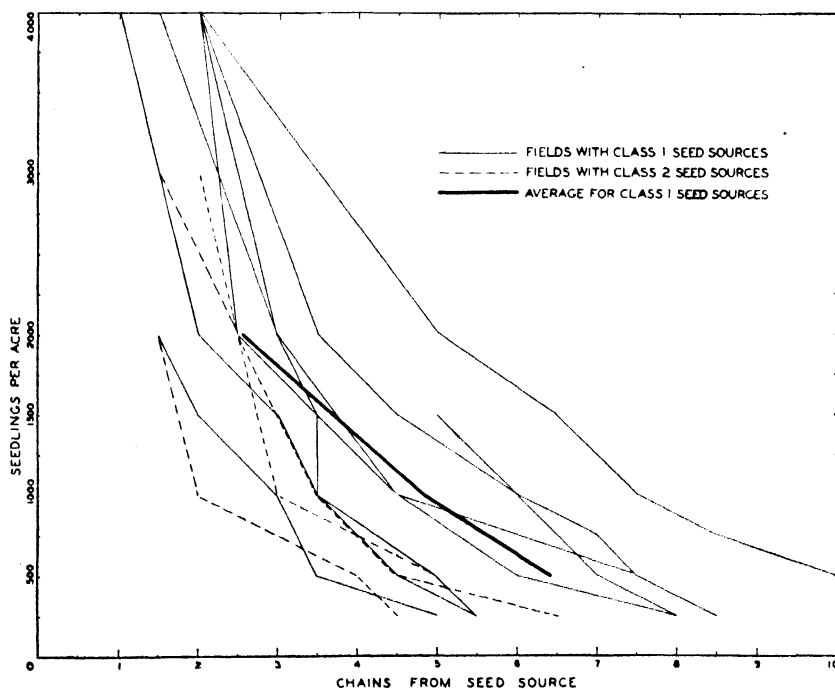
Fig. 4.   Density gradients for all the fields abandoned 4 to 12 years that are listed in table 1.

000, 1,000, and 500 seedlings per acre for the 15 fields above mentioned, together with other descriptive data. Density gradients for the fields listed in the table as abandoned four years or more, and the average gradient for those with class 1 seed sources, are shown graphically in figure 4. Fields abandoned four years or more are grouped together because differences in stocking were too small to justify further division with respect to time since abandonment.

It should be emphasized that the fields included in table I exemplify the best stocking reasonably to be expected under the conditions generally prevailing in the region. The averages shown are only for fields with class 1 seed sources; the 4 fields with class 2 seed sources are excluded from the averages, but are included in the table as illustrations of the best stocking to be expected from seed sources of that quality. The table indicates that on the average a density of 1,000 seedlings per acre is not likely to appear at distances greater than 5 chains from the source of seed, and that a density of 500 seedlings per acre is not likely to appear at distances greater than approximately 7 chains. When, furthermore, it is realized that fields adjacent to good seed sources are decidedly in the minority throughout the Piedmont region, it becomes obvious that widespread and general establishment of stands by natural seeding cannot take place within any such time·interval as 5 or 10 years.

### Differences in habitat

It is evident from table I, and in full agreement with general field observations, that good natural stocking is not restricted to any particular type of soil. The high proportion of soils generally considered of low productivity for agricultural crops, particularly the Iredell and Alamance, is regarded merely as reflecting a higher incidence of abandonment and a higher incidence of older, seed-producing stands on those series. Only a few fields were observed where soil characteristics ap-

peared to be inhibitory to pine establishment, and in these the evidence was not wholly conclusive. In the main, and despite the fact that soil type may be an important factor in the subsequent growth of pine, apparently it is seldom the controlling factor in seedling establishment.

Soil erosion in at least a moderate amount is typical of abandoned farm land throughout the Piedmont. On many fields, the surface soil has been completely removed in places, exposing the clay of the B horizon in "galled" spots. Elsewhere, varying amounts of the A horizon remain, usually somewhat intermixed with B material by cultivation. Frequently, some gullying also has taken place. In the present study, "slight erosion" denotes conditions where a reduced but practically complete mantle of the original A horizon remains; "moderate" denotes the presence of galled spots, gullies, or both; "severe" denotes practically complete loss of the A horizon. Areas entirely devastated by deep, chasm-like gullies constitute an extreme situation outside the scope of this work.

Reference to table I shows that soil erosion within rather wide limits does not preclude invasion of pine. Loss of the original surface soil material and exposure of the B horizon seems in itself to have little effect on pine seedling establishment, except where the structure and composition of the exposed clay are such that it forms when dry an extremely hard, compact, and more or less cemented surface. Erosion may inhibit establishment mechanically by washing away seeds and seedlings before they become firmly rooted, but usually this happens only very locally, as in gully bottoms, and seldom occurs on larger areas. Pine seedlings commonly display a remarkable facility in taking hold despite erosion so active that other vegetation is largely unable to invade (fig. 5).

In general, if seed is supplied in adequate quantity, pine can invade under all but the most severe degrees of soil erosion normally found in old fields. Erosion

FIG. 5. Pine seedlings becoming established on a "galled" spot so severely eroded that most herbaceous plants are unable to invade. The vine near the camera case is the "wild potato" (*Ipomoea pandurata*).

may so modify the habitat that the density of invasion or the time required for attaining a given density is affected, but only rarely does it become the controlling factor in seedling establishment. However, this in no sense implies that soil erosion may not adversely affect tree growth beyond the seedling stages.

The cover of herbaceous vegetation on old fields varies with time since abandonment, and with the amount of erosion that has occurred. The normal herbaceous plant succession, where several inches of natural topsoil remain, is initiated by annual weeds, passes rapidly through a second weed stage, and culminates, usually within 5 years, in a broom sedge (*Andropogon virginicus* L., *A. ternatius* Michx., *A scoparius* Michx.) associes. This stage persists indefinitely, giving way only after trees have appeared and developed a closed canopy. Plant cover may be sparse or practically absent on areas undergoing very active erosion. Where washing is less violent but where most or all of the A horizon has been lost, the pioneer vegetation is an annual weed community dominated by bracted plantain (*Plantago aristata* Michx.), poverty grass (*Aristida dichotoma* Michx.), and buttonweed (*Diodella teres* (Walt.) Small), either singly or in mixture. Successional prog-

ress on poor sites typically remains indefinitely arrested at this stage. Ultimately, as the soil gradually undergoes improvement through vegetational reaction, broom sedge begins to invade, but the above-mentioned annuals usually persist as interstitial species long after dominance has passed to the *Andropogons*. If prolific seed trees are present, pine may follow the poor-site annuals directly, completely excluding the *Andropogon* stage from the succession.

The vegetation type designations for the 15 fields in table I represent fairly well the range of ground cover conditions found in old fields. *Andropogon* generally is dominant in all except recently abandoned or severely eroded areas. Goldenrod (*Solidago nemoralis* Ait.) and thoroughwort (*Eupatorium hyssopifolium* L.) are the most frequently associated species. Trumpet creeper (*Bignonia radicans* L.), daisy fleabane (*Erigeron ramosus* (Walt.) B. S. P.) and, in the lower Piedmont, another goldenrod (*Solidago pinetorum* Small) also are common subdominants. The cover in field S. C. 28 (second year of abandonment), is dominated by *Aster pilosus* Willd. This plant characterizes the second weed stage of the succession on better soils. Field S. C. 24 is an example of severe erosion, nearly

Fig. 6. Excellent natural establishment of pine in an eroded field where the herbaceous cover is predominantly bracted plaintain after 8 years' abandonment. Note also the two age classes in the parent stand in the background. The wide spacing of the older trees is a result, probably, of inadequate seed source at the time the stand originated; subsequently the second age class appeared after the older trees reached cone-bearing age.

all of the A horizon having been lost over practically the entire field. Here, after 8 years of abandonment, the cover is predominantly bracted plantain and buttonweed. *Andropogon* is represented by only occasional small bunches. If left undisturbed, this field will pass directly into forest without a typical *Andropogon* stage ever having appeared (fig. 6).

Although on the older fields much of the pine may have started before, or coincident with, the development of the *Andropogon* stage, it is not uncommon to find seedlings starting beneath a fully established stand of the grass. Apparently they can become established, at least in some years, in all of the herbaceous cover types ordinarily found on abandoned farm land. Invasion of pine is possible because old-field herbaceous vegetation typically is characterized by low densities, depauperate growth, or both. Even in the best developed *Andropogon* types the bunches are rather widely spaced. Den-

sities (basal area occupied) were estimated in most cases to be well below 20 per cent. Because of the open nature of the cover, pine seeds can always reach mineral soil, and light intensities on the ground are practically everywhere well above the tolerance of the pine. The competition created by the herbaceous cover is to a large extent compensated by its protection of the soil and seedlings. Pessin ('38), working on the southern coastal plain, was unable to demonstrate significantly lower contents of soil moisture on grass-covered than on denuded plots. If this holds true in the Piedmont also, it would imply that seedling establishment should not be appreciably inhibited by a grass cover, despite the fact that subsequent growth may be retarded by competition for factors other than soil moisture.

It was observed that seedlings seem unable to start under a very dense, luxuriant cover such as is occasionally found in ra-

vines or where topsoil has been accumulated in building terraces. Here light conditions probably become critical. With these exceptions, type and density of herbaceous cover, within the limits usually found on old fields, do not seem greatly to affect the invasion of pine through competitive reactions. However, these factors may possibly have an indirect effect on pine invasion through the activities of certain seed-eating birds and rodents. Pine seeds and seedlings presumably are subject to the greatest depredations in areas of densest or otherwise most attractive cover. Although a number of birds and rodents are known to be destructive of both seeds and seedlings of pine in artificial plantings, the extent of their damage to natural reproduction is largely speculative. In all probability it is considerable, at least in some years, in areas that favor heavy bird or rodent populations.

Steepness of slope, aspect with reference to cardinal compass points, and topographic position, though frequently correlated with distinct differences in composition and luxuriance of vegetation in mountainous country, are relatively unimportant in the Piedmont because of the gently undulating character of the terrain. The steeper slopes, higher ridges and knolls, and lowlands subject to overflow, which may exert marked effects on vegetation, are, for the most part, still in forest and thus outside the scope of the present problem. In general, topographic features of abandoned fields are distinctly subordinate to other factors in controlling pine establishment.

Soil type, erosion, plant cover, slope, aspect, and topographic position all function indirectly, *i.e.*, they affect plants only as they modify such direct factors as mineral soil nutrients, soil moisture, soil aeration, light, and temperature. Furthermore, the indirect factors must be considered collectively because of compensating effects which may largely counteract the influence of an individual factor. For example, the favorable effects

of lower topographic position or of level surface may be nullified by poor drainage; favorable effects of good soil may be largely counteracted by competition from more luxuriant herbaceous vegetation; conversely, the unfavorable effects of erosion may be compensated to a considerable extent by reduced plant competition.

Soil moisture is doubtless the most critical direct habitat factor affecting the establishment of pine seedlings in old fields. All observations indicate that most seedling mortality occurs during the first few months after germination, and that surface soil moisture is the primary factor affecting it. Hence, in considering only seedling establishment, the complex of site factors should be evaluated primarily in relation to soil moisture.

Very few fields are so unfavorable from the standpoint of site as to preclude satisfactorily dense pine establishment. As a rule, effects of site seriously restrict invasion only in such extreme situations as stony knolls, severely galled spots, gullies, and densely vegetated low terraces or ravine bottoms. These conditions, when present, usually prevail only over small areas of from one-twentieth to one-fourth acre lying within fields otherwise amenable to pine establishment. Site, in terms of soil moisture relations, therefore is to be regarded generally as a secondary factor influencing density, uniformity, and rapidity of pine invasion, and definitely subordinate to seed supply in determining whether satisfactory natural stocking will take place.

*Time required for establishment of pines*

The number of years required for fields with adequate seed sources to become satisfactorily stocked is of course influenced by site conditions. The higher mortalities associated with unfavorable sites increase the time required to attain a given density. However, most of the seedlings in the young stands commonly become established in one, or perhaps two, mass waves of invasion, rather than by a proc-

ess of gradual infiltration. Often a con-
spicuous majority of the young trees date
to one specific year, with the other years
since the abandonment of the field repre-
sented by only relatively small numbers
of seedlings, or none. Sometimes mass
invasion occurs promptly after abandon-
ment, sometimes it is delayed for several
years. As noted previously in discussing
table I, differences in density of stocking
attributable to time since abandonment
generally are negligible in fields aban-
doned 4 years or more. Further refer-
ence to table I shows that differences
between the averages for fields abandoned
1–3 years and those abandoned 4–12 years
are relatively small. From this it may
be inferred that, with good seed sources
and fair to good site conditions, the ma-
jority of the seedlings tend to appear in
one primary wave of invasion during the
first 3 years of abandonment, after which
only slight increases in density take place.
Within this comparatively short period of
time, fluctuations in the quantity of seed
produced from year to year have an im-
portant bearing upon the date of seedling
establishment. Loblolly pine, though it
may produce some seed every year and
is generally regarded as a prolific species,
tends to bear heavily only every second
to fourth year (Pinchot and Ashe, '97;
Ashe, '15; Cope, '23). Shortleaf pine
displays similar rhythmic tendencies (Pin-
chot and Ashe, '97), but according to
Ashe ('15) is less regular and less prolific

in its seeding than loblolly. A heavy seed
crop followed by an adverse growing sea-
son cannot result in good reproduction
except on the most favorable sites; a good
growing season following a poor seed
year is similarly ineffective. It is evident
that the occurrence of a good seed year
followed by a favorable growing season is
largely a matter of chance, and that the
general tendency for a high proportion of
the seedlings on any one field to be of the
same age doubtless results from such
chance circumstances. Also, it is mostly
these same chance circumstances that de-
termine whether a given field shall un-
dergo a mass invasion by pine immedi-
ately after abandonment, or in some later
year.

In fields where severe erosion, poor
subsoil drainage, or other factors create
extremely adverse site conditions, weather
is more important, and the circumstances
necessary for establishment of seedlings
in large numbers occur less frequently.
Such areas may require as much as 10
years to attain a satisfactory density of
stocking. Furthermore, the young stands
are likely to be spotty, and the distance to
which the seed source is effective is in-
clined to be less because of the generally
higher percentage of mortality.

When the seed source is of poor qual-
ity, not enough seed is ever dispersed in
any one year to produce a mass invasion
of adjacent fields, and invasion is more
likely to be a process of gradual or inter-



Fig. 7. Wide spacing of young trees in an abandoned field because of
inadequate seed supply. Full stocking will be attained only after these trees
reach cone-bearing age. See also fig. 6.

mittent infiltration, with the resulting stand typically spotty, understocked, and uneven-aged. Full stocking usually is not attained until the young trees themselves begin to bear seed. Under such circumstances the older trees tend to assume undesirable "wolf" characteristics, those starting 15 to 30 years later are more or less seriously suppressed, and both the quantity and the quality of the timber produced fall far below the inherent capacity of the land (fig. 7).

### Comparison of pine species

All three of the important Piedmont pines—loblolly, shortleaf, and Virginia—reproduce readily in old fields. No marked differences in reproductive vigor of loblolly pine and shortleaf pine are apparent from field observations when each species is well within its natural range. However, where ranges overlap, one species may be closer to its limits, in terms of environmental factors, than the other and consequently more responsive to site differences and generally less aggressive in invading open areas. For example, though both species are abundant, shortleaf pine appears to be distinctly less aggresive than loblolly pine in a section of the lower South Carolina Piedmont extending through Newberry, Saluda, Edgefield, and parts of McCormick and Greenwood Counties. Loblolly pine may be slightly favored by its larger seeds and its tendency to bear them more prolifically (Ashe, '15), but the readiness with which short leaf pine reproduces in the upper and northern Piedmont regions indicates that comparative reproductive vigor of the two species is largely determined by specific adaptations to local environment. Although but little attention was given to Virginia pine, it appears from general observations to be equally aggressive within its natural range.

### Successional relations

Discussion of the general trends and predominant species of old field herbaceous succession is outside the scope of this paper. Observations and comments made here pertain primarily to the successional relations of pine.

Since forest vegetation is generally regarded as more mesophytic and successionally more advanced than herbaceous types, it might logically be expected that the establishment of pine would be conditioned by, and would follow, one or more herbaceous stages. This interpretation of old field succession in the Piedmont has been stated or inferred in the rather meagre literature of the subject. According to Crafton and Wells ('34) the "broom-sedge invades—reaches its extreme expression—then passes out with the ecesis of pines." The same view is expressed elsewhere by Wells ('32), together with a positive statement that pines do not invade fields until after the herbaceous stages have developed. There is an abundance of evidence to challenge the unqualified applicability to Piedmont fields of this conventional concept of succession.

It is true that, with fair to good soils, dominance in old-field vegetation typically passes from annual weeds to perennial weeds, to *Andropogon*, to pine. It does not follow, however, that a similar succession of invasion or ecesis prevails. Pines may come in during the first year of abandonment or during any succeeding year when seed supply and weather are favorable. Pine seedlings remain relatively small and inconspicuous through their first two or three years, and are relatively undemanding of both soil and space. They do not interfere with the normal progress of the herbaceous succession; nor are they dependent on it. Each apparently develops independently of the other. Pines seem fully as capable of colonizing bare areas as the hardiest weeds and, as previously noted in the discussion of erosion and vegetal cover, they may become established on eroded areas so far in advance of *Andropogon* that the latter is completely excluded from the succession. The normal succession to pine on the better soils therefore is primarily a succession of dominance only,

and results from the fact that the entire sequence of herbaceous stages has ample time to develop before the pines are large enough to assume the controlling role. Invasion of the pines ordinarily is conditioned but little, if at all, by the herbaceous vegetation.

The evidence in support of the above contention consists of: (1) numerous unrecorded observations of pines coming in on galled spots and other bare areas where herbaceous cover was sparse or lacking; (2) plot records showing fair to good densities of reproduction on fields so severely eroded that the succession of *Andropogon* was indefinitely delayed, *e.g.*, field S. C. 24, table I; (3) plot records showing fair to good densities of reproduction dating wholly or in large part to the first or second year of abandonment, *e.g.*, Fields S. C. 8 and S. C. 28, table I; (4) plot records of 4 first-year fields showing the general presence of live seedlings, and as many as 30 on one 4-milacre plot; (5) many unrecorded observations of pine seedlings starting and surviving in all stages of the herbaceous succession.

Although as a rule trees are not expected to appear until late in plant successions, the ability of loblolly pine and shortleaf pine to become established over a wide range of old field soil and vegetational conditions is not inconsistent with the ecological characteristics of the species and habitats concerned. In the first place, the pines are not climax species with highly exacting habitat requirements. In the Piedmont they occupy pre-climax and sub-climax positions, and therefore are adapted to situations less mesic and less fertile than those generally prevailing within climax communities, or on virgin soils. They have many of the attributes of weed or pioneer species, particularly in their relatively low tolerance of the conditions found under a forest canopy, in their adaptation to dry, open sites, and in their ability to withstand direct insolation.

Secondly, old fields represent not priseres, but subseres, as defined by Weaver and Clements ('29). The expression "old-field prisere," as used by Crafton and Wells ('34), seems to be an inappropriate choice of terms. "Prisere" denotes a primary sere or succession beginning in open water, bare rock, sterile sand, etc.; "subsere" denotes a sere following denudation of an established natural vegetation where the effects of that preceding cover have not been wholly destroyed. Old-field soils in the Piedmont, even when eroded, still embody in their structure and composition the accumulated reactions of innumerable generations of plants, and thus constitute habitats developed far beyond the early stages of a prisere. Consequently, the succession starts with an advanced stage, and progresses with but few steps to the climax. The evidence found in this study seems ample to justify the following interpretation: (1) that Piedmont fields sufficiently retain the properties of ecologically mature habitats for succession to begin with pine; (2) that the herbaceous succession in these fields plays an entirely subordinate role insofar as ecesis of pines and reversion to forest are concerned. Although herbaceous cover undoubtedly exerts some influence as a protection against erosion, as a competitor of pine seedlings, or in other less direct ways, there is no reason to regard it as a fundamental or essential step in the transition from fallow field to forest.

## SUMMARY

1. The paramount factor affecting establishment of loblolly pine and shortleaf pine in abandoned fields in the Piedmont region is the presence of an adequate source of seed. An adequate source of seed is defined as a stand of pine 40 years or more old and 50 per cent to fully stocked, in which the individual trees, or at least those at the edge of the stand near the field, are characterized by vigorous growth, well developed crowns, and abundant cone production. The parent stand should extend along at least one entire side of the field.

2. The site factors (soil type, degree of

erosion, steepness of slope, aspect, topographic position, and type of herbaceous vegetation) may, by affecting the supply of available surface soil moisture, account for variations in densities of established seedlings or in the time required for a given density to be attained, but in general they are not controlling factors in the establishment of pine on abandoned land.

3. With adequate seed sources and fair to good site conditions in the fields, pine reproduction in densities equivalent to 1,000 or more seedlings per acre is found to distances averaging about 5 chains (330 feet) from the parent stand. Densities of 500 or more seedlings per acre are found to distances averaging about 7 chains. Beyond 7 chains from the parent stand, seedling establishment usually is erratic and uncertain, and seldom approaches satisfactory densities.

4. Invasion of pine into abandoned fields in the Piedmont is not conditioned by, nor directly related to, the succession of herbaceous plants. Pine may invade fields immediately after abandonment or at any time thereafter when seed is supplied and weather conditions are favorable. With a good seed source present, stocking to the densities and distances above indicated may occur within 3 to 5 years; seldom does it require more than 10 years. Chance coincidences of good

seed years followed by favorable weather conditions are important determinants of the length of time required for fields to become satisfactorily stocked.

5. The greatest obstacle to prompt natural reforestation of abandoned farm land in the Piedmont lies, not in the inability of pine to become established under ordinary field conditions, but in the widespread deficiency of natural seed supplies following cutting of the older stands. Because of lack of seed trees, much artificial planting will be necessary if the productive capacity of the land is fully to be utilized.

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# THE SOCIAL HIERARCHY IN RING DOVES. II. THE EFFECT OF TREATMENT WITH TESTOSTERONE PROPIONATE [1]

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## INTRODUCTION

Social organization has been described in flocks of many species of birds both wild and caged. Schjelderup-Ebbe ('24, '31) reported in more than fifty species a type of hierarchy which he designated as a "peck-order." Subsequent investigation by others has confirmed his observations with relation to the domestic chicken (Masure and Allee, '34a; Murchison, '35). In the case of pigeons and shell parrakeets, Masure and Allee ('34b) reported a social order based upon "peck-dominance" rather than peck-right, that is, upon a dominance established after many conflicts rather than upon an initial combat. Shoemaker ('39a) and Bennett ('39), in flocks of canaries and of ring doves respectively, likewise found peck-dominance to be characteristic of the social organization in caged flocks of these birds. Others who have observed hierarchies in bird flocks, based upon dominance in some form, are Lorenz ('35) in jackdaws, geese, and certain other birds, both in wild and artificial associations, and Noble, Wurm, and Schmidt ('38) in American black crowned night herons.

The question arises as to what factors underly the social organization in a flock of birds. Schjelderup-Ebbe ('35) directed attention to a number of conditions which he believed to be of some importance in this matter. Among them were health, season, sex, age, relative strength and fatigue. Certain of these same conditions have been recognized by other investigators. Allee, referring to the do-

mestic hen, says, "Sickness limits the social activity of a bird and may result in a loss of social position" (Allee, Collias, and Lutherman, '39). In wild flocks, season operates in relation to the breeding cycle. In that sense season is probably of significance in flock control. Shoemaker ('39a) found in caged canaries that "position in the social hierarchy fluctuates with breeding activity." Age has been reported as affecting the social status of chickens when immature and mature individuals are both present (Allee, '38). In canaries, Shoemaker failed to find a correlation between age and social position. Homosexual flocks of ring doves, sexually mature, and healthy according to ordinary criteria, have been observed in this and previous investigations (Bennett, '39) at all seasons of the year. In these flocks, it appeared that the elimination of differences in such conditions as health, sex, and age, at least in the ordinary usage of these terms, did not greatly modify the flock order.

Some degree of recognition of individuals is implied in any social organization. By an analysis of the factors involved, a better understanding of that organization should be possible. The senses of hearing and sight are well developed in birds. Certain studies of these in relation to recognition have been made. Craig ('08) found in doves and pigeons a marked effect of "voice" upon flock activity. Much of this was of a transitory nature. Gross changes in appearance, so far as the effect of altered coloration of plumage and modifications of contour were concerned, produced negligible results (Bennett, '39). Flock organization was only temporarily disturbed. The doves seem to be aware of changed appearances but to base recognition of individuals on some more innate factor or factors. Human

observers have considerable difficulty in distinguishing sexes in ring doves because of the lack of external, morphological differences. The birds themselves seem unable to readily determine the sex of new arrivals until initial responses to approaches have been made. Whitman ('19) said, "The behavior is the only guide they have in selecting a mate of the right sex." It is probable in flock organization, as in sex, that recognition is based upon behavior characteristics. With modification of behavior, changes in responses are to be expected, and more or less alteration of relationships in the flock.

Some experimental work in the modification of the social order in bird flocks, as well as of other conditions, has been done. It has been based upon the idea that the degree of pugnacity and aggressiveness, which enables a bird to maintain its social position, is dependent, at least in part, upon the relative amount of "maleness" possessed by it. Whitman reported a frequent occurrence of fighting in homosexual ring dove pairs. Riddle (Whitman, '19) commented upon this observation by postulating that such combats in either sex were probably due to varying degrees of maleness. More recently Allee ('36) suggested that sex hormones might "alter experimentally the physiological state of selected birds of known status in the social group" and, incidentally, the social order as well. It has been shown that aggressiveness in female birds can be enhanced by the injection of male hormone. Allee and co-workers (Allee and Collias, '38; Allee, Collias and Lutherman, '39) observed such changes in flocks of hens, as well as a resultant modification of social status, after injection of testosterone propionate. The work of Shoemaker ('39b) with canaries confirms their results. Noble and Wurm ('38) in black crowned night herons, Hamilton and Golden ('39) with hens, and Leonard ('39) with canaries, have verified the idea that testosterone propionate produces behavior in female birds of a definite male pattern.

The present investigation has had as one of its purposes an attempt to discover whether the injection of testosterone propionate in ring doves, birds possessing a well defined peck-dominant type of organization, would parallel the developments in hens and other birds under similar treatment. In the second place, if such parallelism resulted, it was planned to repeat the procedure used in as nearly an identical manner as might be practicable. The purpose of such repetition was that of securing further evidence necessary to valid conclusions in birds with a flexible social organization. A single series of results, while apparently confirming those obtained in chickens where the peck-order prevails, might in birds with a peck-dominant organization, as is the case with doves, be a matter of chance. Repetition of the experimental procedure would assist in clearing the picture, either confirming or raising a question as to the conclusions to be drawn. A third matter for investigation has been the question as to whether, with injection of testosterone propionate, there might appear a change from the peck-dominant to the peck-right form of organization in the ring dove flocks concerned.

Both male and female flocks were used. If, as Riddle suggested, and as subsequent investigations have seemed to show, the degree of maleness in either sex is an important factor in aggressiveness, modification by injection of male hormone should have effects in male as well as female flocks.

## METHODS AND MATERIALS

The procedure in this investigation, so far as the general care of the birds was concerned, varied little from that in the preceding one (Bennett, '39). Caged flocks, seven birds in each, were used. One flock was of females and two of males. Male flock *B* was composed of doves raised by the investigator, and the

offspring of two related pairs. The ages in this flock varied but four months. The other birds were obtained from commercial sources. All in the three flocks were sexually mature when used. Individuals were permanently identified by metal bands but marked with colors for ready recognition. The flocks received daily care with regard to food, water and cleanliness. In the summer they were housed within Whitman Laboratory, in the fall months in the greenhouse of the same building.

Recorded observations, an hour each per flock, were made daily. (At times of lessened activity, these could be made simultaneously for more than one flock; much of the time each required separate records.) In addition, particularly during the summer, the flocks were under observation much of the remainder of the time during daylight hours. By working quietly in the neighborhood of the birds, any unusual conditions could be checked.

The three flocks, with the same individuals in each, were maintained throughout the investigation. The reported observations began June 27, 1939, but an earlier series made in April were available for comparison. The summer observations, series I, ended September 12 after seventy-eight days of continuous records. Series II began October 3, and ended November 21, fifty days in all. The pre-

injection or control, the injection, and the post-injection periods within each series, are shown in table I. The pre-injection or .control period of eight days was arbitrarily fixed at this length since results in all previous studies of ring doves (Bennett, '39) had seemed to indicate as accurate a picture of any given flock organization, in an undisturbed condition, in this period as in those of greater length. The pre-injection period of series II proved of double use, both as a check upon the post-injection conditions for series I and as a control for series II. In the injection period of series I, one bird in each flock was treated continuously for forty-eight days. Beginning on the thirty-fifth day of these injections, an additional bird each in male flock A and in the female flock were treated for twenty-four days. While twenty-one days' post-injections in the first three cases were possible, only ten days could be used for the latter two. In series II, three of the originally treated birds, one from each flock, were again the experimental subjects. The periods were similar for all. The control period was eight days as in series I. The following two intervals were somewhat curtailed in length.

The experimental birds were selected, not only upon the basis of their ranks and behavior in the control period, but also

TABLE I. *Calendar of observations in flocks of ring doves, 1939*

| Doves | | Series I | | | Series II | | | |
|---|---|---|---|---|---|---|---|---|
| Name of treated bird | Flock | Pre-injection | Injection | Post-injection | Pre-injection | Injection | Post-injection | Total days |
| | | 8 da. | 48 da. | 21 da. | 8 da. | 24 da. | 17 da. | |
| X | A ♂ | 27.vi–5.vii | 16.vii–22.viii | 23.viii–12.ix | — | — | — | 77 |
| EB | B ♂ | 27.vi–5.vii | 16.vii–22.viii | 23.viii–12.ix | 3.x–10.x | 12.x–4.xi | 5.xi–21.xi | 126 |
| D | ♀ | 27.vi–5.vii | 16.vii–22.viii | 23.viii–12.ix | 3.x–10.x | 12.x–4.xi | 5.xi–21.xi | 126 |
| | | 8 da. | 24 da. | 10 da. | | | | |
| RW | A ♂ | 1.viii–8.viii | 9.viii–2.ix | 3.ix–12.ix | 3.x–10.x | 12.x–4.xi | 5.xi–21.xi | 126 |
| RH | ♀ | 1.viii–8.viii | 9.viii–2.ix | 3.ix–12.ix | — | — | — | 77 |

as a result of their performances previous to the reported observations. These doves were, so far as could be determined, the least aggressive individuals in their respective flocks, and the birds most consistently low in rank. It was important to consider consistency in status since certain ring doves, in almost all caged groups observed, have shown an erratic type of flock relationship. *EW* in male flock *B* in the present investigation is an example of this sort. If such a bird, with a tendency to change readily in flock position, were to be used experimentally, it is clear that it would be difficult to interpret results in his case.

During the experimental periods, testosterone propionate was injected daily, intramuscularly, in the subjects. All other birds received similar treatment with sesame oil. The original daily dosage used was 0.25 milligrams, but this amount was doubled in all males after twenty-four days. Since the apparent female response remained practically maximum, once it reached this peak, it was deemed unnecessary to increase the amount of hormone used. A change in the males, since such a maximum response was not indicated, was made in the attempt to learn whether insufficient dosage was responsible.

## MODIFICATION OF THE SOCIAL HIERARCHY FOLLOWING INJECTION OF TESTOSTERONE PROPIONATE

The history of each flock and of each treated bird in series I is discussed sep-

TABLE II.   *Order in peck-dominance in the female flock of ring doves as modified by injection of bird D with male hormone. Double vertical lines enclose the injection periods*

Series I

| Doves | 8 da. | 0.25 mgm. | | | | | 21 da. |
|---|---|---|---|---|---|---|---|
| | | 8 da. | 8 da. | 16 da. | 16 da. | Total | |
| D:C | 2:1 | 0:1 | 0:1 | 9:2 | 1:2 | 10:6 | 11:6 |
| D:RH | 0:0 | 0:1 | 2:0 | 0:5 | 0:1 | 2:7 | 7:4 |
| D:T | 0:0 | 0:2 | 0:6 | 0:28 | 0:21 | 0:57 | 1:5 |
| D:E | 5:0 | 4:0 | 4:3 | 0:27 | 0:39 | 8:69 | 0:17 |
| D:G | 0:0 | 3:12 | 0:22 | 1:89 | 1:71 | 5:194 | 0:28 |
| D:S | 0:0 | 0:0 | 0:1 | 0:13 | 0:3 | 0:17 | 0:6 |
| C:RH | 0:0 | 0:3 | 0:0 | 0:2 | 4:1 | 4:6 | 16:4 |
| C:T | 1:0 | 4:1 | 7:0 | 7:2 | 9:11 | 27:14 | 11:2 |
| C:E | 0:1 | 0:1 | 0:7 | 1:16 | 0:9 | 1:33 | 1:20 |
| C:G | 0:8 | 0:2 | 0:11 | 0:19 | 0:6 | 0:38 | 0:34 |
| C:S | 2:1 | 2:0 | 5:1 | 0:23 | 1:7 | 8:31 | 1:23 |
| RH:T | 0:0 | 0:2 | 0:11 | 0:3 | 0:53 | 0:69 | 0:40 |
| RH:E | 0:0 | 0:1 | 1:0 | 2:0 | 6:13 | 9:14 | 0:10 |
| RH:G | 0:1 | 4:0 | 4:1 | 9:0 | 33:1 | 50:2 | 4:2 |
| RH:S | 0:0 | 0:0 | 2:0 | 0:0 | 2:9 | 4:9 | 0:9 |
| T:E | 2:2 | 0:3 | 0:3 | 8:6 | 0:5 | 8:17 | 2:8 |
| T:G | 1:3 | 1:2 | 1:0 | 7:3 | 21:1 | 30:6 | 9:11 |
| T:S | 0:1 | 0:0 | 0:1 | 2:0 | 0:3 | 2:4 | 0:10 |
| E:G | 0:0 | 4:3 | 0:4 | 0:4 | 2:8 | 6:19 | 2:20 |
| E:S | 0:0 | 1:0 | 1:1 | 0:8 | 2:5 | 4:14 | 0:7 |
| G:S | 1:0 | 2:0 | 1:0 | 7:1 | 2:0 | 12:1 | 0:10 |
| Total | 14:18 | | | | | 190:627 | 65:276 |
| Rank in Flock | T(3.5)<br>C(3)<br>S(2)<br>E(1.5)<br>RH(1)<br>G,*D*(0) | *D*(4)<br>C,T,S(3)<br>G,RH(2)<br>E(1) | *D*(4)<br>E,S(3.5)<br>T(3)<br>G,C,RH(2) | *D*,C(5)<br>E(4)<br>G,S(2)<br>RH,T(1) | *D*(6)<br>C(4)<br>E,RH(3)<br>G,T(2)<br>S(1) | *D*,C(5)<br>RH,T(3)<br>G,E(2)<br>S(1) | RH(5)<br>*D*,C,T(4)<br>G,E(2)<br>S(0) |

TABLE II   (*Continued*)

Series II

| Doves | 8 da. | 0.25 mgm. | | | 17 da. |
| --- | --- | --- | --- | --- | --- |
| | | 8 da. | 16 da. | Total | |
| D:C | 7:0 | 3:1 | 7:13 | 10:14 | 8:8 |
| D:RH | 5:0 | 6:5 | 3:9 | 9:14 | 1:14 |
| D:T | 1:0 | 0:5 | 2:23 | 2:28 | 0:24 |
| D:E | 0:3 | 0:2 | 1:46 | 1:48 | 0:17 |
| D:G | 0:6 | 1:19 | 0:62 | 1:81 | 0:19 |
| D:S | 0:0 | 0:8 | 4:37 | 4:45 | 0:24 |
| C:RH | 3:1 | 0:3 | 2:6 | 2:9 | 6:2 |
| C:T | 1:0 | 0:0 | 7:2 | 7:2 | 8:5 |
| C:E | 0:10 | 1:1 | 3:26 | 4:27 | 0:27 |
| C:G | 1:22 | 0:4 | 1:11 | 1:15 | 1:23 |
| C:S | 0:14 | 0:8 | 0:23 | 0:31 | 0:26 |
| RH:T | 0:0 | 0:1 | 0:6 | 0:7 | 0:6 |
| RH:E | 0:0 | 0:0 | 3:1 | 3:1 | 1:1 |
| RH:G | 0:0 | 0:0 | 6:2 | 6:2 | 7:0 |
| RH:S | 0:0 | 1:1 | 4:2 | 5:3 | 0:0 |
| T:E | 1:0 | 0:0 | 2:1 | 2:1 | 2:3 |
| T:G | 2:1 | 1:0 | 26:0 | 27:0 | 21:0 |
| T:S | 0:1 | 0:2 | 4:7 | 4:9 | 2:3 |
| E:G | 5:5 | 3:2 | 12:3 | 15:5 | 19:4 |
| E:S | 0:7 | 0:2 | 2:11 | 2:13 | 7:6 |
| G:S | 2:20 | 0:8 | 4:27 | 4:35 | 1:29 |
| Total | 28:90 | | | 109:490 | 84:241 |
| Rank in Flock | C(4) T(3) G,E(2.5) D,RH(2) S(0) | C(4.5) D(4) G(3) RH(2.5) E(1.5) T(1) S(.5) | D(6) G,C(4) E(3) T(2) RH,S(1) | D(6) G,C(4) E(3) T(2) RH,S(1) | D(5.5) G(4) C(3.5) T(3) RH(2.5) S(1) E(.5) |

arately since the condition in each varied somewhat. In the tables accompanying each record, individual birds are represented by letters. The successive columns of figures give the number of times of observed peck-dominance in the indicated contact pairs for the period shown. In table II, for example, *D*'s contacts with *C* in the pre-injection period are recorded as 2: 1. *D* won in one encounter as contrasted with two winning contacts on *C*'s part. For the total injection period of forty-eight days, the comparative winning contacts are listed as 10: 6, that is, six in *D*'s case, and ten in *C*'s case. *C* is said to be peck-dominant in both periods. The rank in the flock, shown in the latter part of each table, is determined according to the number of other birds over which

any one bird has dominated. This number is shown in parentheses.

*Series I. Female Flock.*—The original experimental female, *D*, was before injection, in the lowest rank (table II). She was an extremely quiet, passive individual, making almost no contacts and those, in large part, losing ones. On the sixth day following injection, *D* had risen a stage in rank, having subjugated one bird. The following day she was discovered in top rank but sharing it with *C* and *T*. On the eighth day, *D* had her first observed pecking contact with *C* following injection, and won it in a decisive manner. This elevated her to an isolated state in first place in the flock. So long as injections continued, *D* remained in first rank, but shared it at times with *C*.

(Once, too, for three days, the tenth to the twelfth, $S$ and $T$ were in the same position.) Five days after injections ceased, $D$ became secondary to $C$. On the eighth day and for the thirteen remaining post-injection days $D$ became subservient to $RH$, but through this period, shared second place with $C$ and $T$. $RH$ was still being injected for eleven days of this period, a fact which probably accounts for her ascendancy over $D$. The data for the twenty-one day post-injection period showed no marked change in $D$'s status, such as occurred in the injection period. The chief modification, too, is involved with the treatment of the second flock member. Less noticeable shifts in relationship were nevertheless in process. An examination of the last five days' data showed $D$ in third rank, if those days alone were considered. Fifty days after cessation of treatment, at the end of the control period in series II, $D$ was found in fourth rank in advance of one bird only.

$D$'s behavior changes were quite striking. From an apparently voiceless and a very submissive bird, she began soon after injections started, a progressively cumulative series of developments which resembled quite closely the steps in typical male dove courting ceremonies (table III). The first evidence of this change observed was somewhat startling in nature. The female flock as a whole had been an unusually quiet one. In the scattered cases where vocalization occurred it was brief in nature and weak in tone. When on the fifth day of $D$'s injection, a strong, clear "bowing-coo" issued from the corner occupied by the cage of the females, it was difficult to attribute this call to one of the birds there. Repetition was convincing, and $D$ was found to be the vocalist. Such behavior became frequent with her in the weeks following. When copulation was attempted by this same bird on the thirty-fourth day, it was the culmination of a succession of appearances of various stages in the male courting pattern. Oc-

TABLE III. *Initial appearance in female ring doves during injection by male hormone of characteristic types of male courting behavior*

| Male courting behavior | Days following first injection | | |
|---|---|---|---|
| | D | | RH |
| | Series I | Series II | Series I |
| 1. Bowing and cooing to second individual | 5 | 1 | 2 |
| 2. Approaching from sides as if to mount | 7 | 5 | — |
| 3. Following courted individual from place to place | 15 | 12 | — |
| 4. Billing | 16 | 5 | 15 |
| 5. Courting arousing reciprocal excitement | 17 | 14 | — |
| 6. Courting followed by "Flattening" on part of other bird | 20 | — | 3 |
| 7. Pecking preceding posturing | 22 | — | — |
| 8. Mounting courted bird | 34 | — | — |
| 9. Mounting, succeeded by attempted copulation | 34 | 16 | — |

curring initially in each case at intervals of several days, each had been a part of a progressive sequence. It may be noted that it required a few days over a month before the summation of all stages appeared in a complete courting pattern climaxed by sexual contact. No further "copulation" on $D$'s part was observed although she was watched closely for considerable periods each day. She was seen on two further occasions to mount other birds but failed to attempt copulation. A different type of observation gives added evidence of a change in a male direction. $D$ was temporarily introduced into the male flocks and into a mixed flock, both during the control period and in the later part of the injection period. Before injection $D$ was courted by the males in the various cages and was herself very passive and irresponsive. After several weeks of injection, she usually took the initiative in encounters, occasionally fighting the higher ranking males viciously. In the mixed flock, she courted other females but fought the males. After cessation of injections $D$ gradually

TABLE IV. *Order in peck-dominance in the female flock of ring doves as modified by injection of bird RH with male hormone. Double vertical lines enclose the injection period. The last column refers to an eight day period of observations ending 39 days after injections ceased*

| Doves | 8 da. | 0.25 mgm. | | | 10 da. | 8 da. |
|---|---|---|---|---|---|---|
| | | 8 da. | 16 da. | Total | | |
| RH:D | 3:0 | 0:0 | 2:3 | 2:3 | 3:3 | 0:5 |
| RH:T | 0:5 | 0:26 | 0:36 | 0:62 | 0:13 | 0:0 |
| RH:C | 0:0 | 1:2 | 1:11 | 2:13 | 3:3 | 1:3 |
| RH:E | 6:0 | 2:8 | 0:9 | 2:17 | 0:5 | 0:0 |
| RH:G | 6:0 | 27:0 | 5:2 | 32:2 | 0:1 | 0:0 |
| RH:S | 0:0 | 2:4 | 0:9 | 2:13 | 0:4 | 0:0 |
| D:T | 0:36 | 0:6 | 0:10 | 0:16 | 1:0 | 1:0 |
| D:C | 6:2 | 0:0 | 6:8 | 6:8 | 6:0 | 7:0 |
| D:E | 0:21 | 0:16 | 0:21 | 0:37 | 0:0 | 0:3 |
| D:G | 0:50 | 1:38 | 0:40 | 1:78 | 0:7 | 0:6 |
| D:S | 0:10 | 0:0 | 0:6 | 0:6 | 0:3 | 0:0 |
| T:C | 4:6 | 8:6 | 3:10 | 11:16 | 0:2 | 0:1 |
| T:E | 4:7 | 0:2 | 1:5 | 1:7 | 1:4 | 1:0 |
| T:G | 8:2 | 15:0 | 13:4 | 28:4 | 0:7 | 2:1 |
| T:S | 2:0 | 0:0 | 0:10 | 0:10 | 0:3 | 0:1 |
| C:E | 0:6 | 0:6 | 1:13 | 1:19 | 0:8 | 0:10 |
| C:G | 0:12 | 0:4 | 0:16 | 0:20 | 0:18 | 1:22 |
| C:S | 0:16 | 1:3 | 0:12 | 1:15 | 1:14 | 0:14 |
| E:G | 0:8 | 2:2 | 0:6 | 2:8 | 2:6 | 5:5 |
| E:S | 0:6 | 2:3 | 0:5 | 2:8 | 0:4 | 0:7 |
| G:S | 7:0 | 2:0 | 0:6 | 2:6 | 0:4 | 2:20 |
| Total | 46:187 | | | 95:368 | 17:109 | 20:98 |
| Rank in Flock | D(5) C(4) E(3) G,T(2) RH,S(1) | C,RH(4) D(3) G(2.5) E(1.5) T,S(1) | D,RH(5) G,C,T(3) E(2) S(0) | D,RH(5) G,C,T(3) E(2) S(0) | RH,T(5) C(4.5) D(2.5) E(2) G(1) S(0) | C(4) T(3) G,E(2.5) D,RH(2) S(0) |

became less aggressive and active. By the tenth day she was found most of the time at the end of a perch. (Developments during the second series of injections will be considered in a later section of the paper.)

The second experimental female, *RH,* until injections began, was, like *D,* consistently low in rank. Unlike *D,* she was a rather active individual. On one occasion she had been observed to bow and coo to another female. Her pecking contacts, in comparable pre-injection periods, were almost as rare as *D*'s. In this period, *RH* was in lowest rank, together with *S* (table IV). Here she remained until the sixth day of injection. On that day she had assumed dominance over four members of the flock and was in second rank with *D.* (*D*'s ranking here

is based on the days of the period concerned in observations of *RH*'s reactions.) On the following day, *RH* shared first rank with *C.* Thereafter she was either in first or second place, in company with or dominating *D,* and always dominating the others of the flock. *RH* continued with *T* in first rank, to the end of the observed post-injection period. Thirty-nine days later, at the close of the control period for series II, *RH* was once more in the lower ranks. Apparently, as in *D*'s case, she had resumed the pre-injection status.

*RH*'s behavior failed to follow the clear-cut progression toward typical male conduct which characterized *D*'s. It may be that the simultaneous injection of the two, one in the later days, the other in the initial stages of the changes following

TABLE V. *Order in peck-dominance in male flock of ring doves A as modified by injection of bird X with male hormone. Double vertical lines enclose the injection period. The last column refers to an eight day period of observations ending fifty days after injections ceased*

| Doves | 8 da. | 0.25 mgm. | | 0.5 mgm. | | Total | 21 da. | 8 da. |
|---|---|---|---|---|---|---|---|---|
| | | 8 da. | 16 da. | 8 da. | 16 da. | | | |
| X:TD | 8:3 | 3:2 | 3:0 | 2:0 | 4:0 | 12:2 | 7:0 | 4:0 |
| X:W | 6:2 | 1:0 | 11:8 | 9:0 | 12:1 | 33:9 | 7:0 | 4:1 |
| X:Z | 10:12 | 2:4 | 7:11 | 2:8 | 4:4 | 15:27 | 21:0 | 15:6 |
| X:FD | 26:8 | 4:8 | 11:20 | 14:14 | 14:5 | 43:47 | 4:0 | 7:6 |
| X:RW | 5:5 | 3:9 | 0:8 | 0:0 | 2:3 | 5:20 | 33:2 | 0:1 |
| X:TB | 1:3 | 1:14 | 7:12 | 2:8 | 7:12 | 17:46 | 3:0 | 0:0 |
| TD:W | 13:3 | 10:8 | 14:16 | 1:6 | 19:9 | 44:39 | 8:9 | 35:5 |
| TD:Z | 11:15 | 11:4 | 4:11 | 0:0 | 6:10 | 21:25 | 37:16 | 9:2 |
| TD:FD | 5:64 | 5:7 | 3:20 | 0:6 | 3:16 | 11:49 | 3:10 | 5:31 |
| TD:RW | 11:20 | 6:17 | 3:16 | 1:7 | 8:8 | 18:48 | 41:17 | 0:32 |
| TD:TB | 5:27 | 7:15 | 5:19 | 0:4 | 1:8 | 13:46 | 0:18 | 0:14 |
| W:Z | 2:12 | 5:14 | 8:37 | 6:19 | 8:28 | 27:98 | 23:7 | 1:11 |
| W:FD | 25:15 | 15:29 | 15:44 | 25:32 | 29:57 | 84:162 | 8:1 | 1:44 |
| W:RW | 0:16 | 7:35 | 32:31 | 11:28 | 24:49 | 74:143 | 33:13 | 0:20 |
| W:TB | 7:8 | 3:29 | 7:31 | 0:9 | 5:47 | 15:116 | 0:4 | 0:14 |
| Z:FD | 12:19 | 3:5 | 23:31 | 7:13 | 16:23 | 49:72 | 13:33 | 6:21 |
| Z:RW | 7:8 | 12:12 | 30:51 | 14:14 | 31:19 | 87:96 | 39:20 | 0:22 |
| Z:TB | 4:9 | 2:7 | 8:31 | 4:15 | 4:16 | 18:69 | 0:38 | 0:7 |
| FD:RW | 7:4 | 1:4 | 6:5 | 1:10 | 10:17 | 18:36 | 29:12 | 1:9 |
| FD:TB | 11:24 | 3:5 | 22:10 | 23:2 | 19:4 | 67:21 | 1:22 | 0:15 |
| RW:TB | 6:14 | 4:5 | 25:15 | 21:8 | 25:13 | 75:41 | 0:51 | 2:1 |
| Total | 182:291 | | | | | 746:1212 | 310:273 | 90:262 |
| Rank in Flock | TD,W(5) Z,FD(3) X,RW(2.5) W(0) | W(6) X,TD(4) Z(3.5) FD(2.5) RW(1.5) TB(0) | TD(6) X,W(4) Z(3) TB,RW(2) FD(0) | TD,W(5) X,Z(2.5) TB(2) FD(1.5) RW(.5) | W(6) TD(4.5) X,Z(2.5) FD,TB(2) RW(1.5) | W(6) TD(5) X(4) Z(3) TB(2) FD(1) RW(0) | Z,RW(5) TD,W(4) FD(2) X,TB,W(0) | W(6) Z(5) TD(4) FD(3) X,TB(1) RW(0) |

treatment with testosterone propionate, complicated the picture. It was at this point that *D* failed to continue the newly developed copulation practice. Then, too, *RH*, as previously noted, had been observed in a preliminary courtship act before being treated. So far as she was watched, *RH* did not attempt the sexual act. She was noted in an attempt to mount on two occasions. After cessation of injections *RH* rapidly became as passive as *D*. By the fifth day she was usually on the perch at *D*'s side. In contrast, the other flock members were quite as active as during the injection periods, changing locations, occasionally pecking one another, and infrequently courting.

*Series I. Male Flocks.*—The bird, *X*, selected from male flock *A* for experimental treatment, was one of the less active birds and in the next lowest rank in the pre-injection period (table V). During that eight-day period he had been observed to win in thirty-seven encounters. After five injections *X* was found with *TD* in second rank and maintained this position to the twentieth day. In the first eight days of injection, *X* had thirty-three encounters. In the preceding period he had had a few more winning contacts but dominated in the total pair contacts in two cases only, those with *Z* and *TB*; in this second period, in four, those with *Z, FD, RW*, and *TB*. The total individual decisive contacts on the part of all birds were ninety-seven in the pre-injection period; forty-seven in the first eight days of injection. Since the increase in *X*'s case was very slight, it appears that it was rather in an avoidance of him, than in increased combat upon his part, that his rise in status took place. Numerous instances were observed in which other males approached him as if for conflict, then hurriedly withdrew as in fear. *X*, himself, seemed to have changed. His pecks were more vigorous; in combats, he appeared to be "standing his ground" with increased assurance. When the entire period of forty-eight days was considered, *X* was found to be in third place and ranking higher than

four other birds. In the pre-injection period $X$ had also shared third place with another bird but had ranked above one bird only. An examination of the data in the various injection columns shows that $X$ was in second rank in the first three of these, when only the days of each individual period are considered. He failed to maintain this position in the final sixteen days of injection although at this time increased dosage was in operation. In the twenty-one day post-injection period, $X$ was observed to win contacts in two cases only. His return to lowest rank was therefore inevitable. As in the female flock, a coinciding injection of a second bird may have been a complicating factor. $RW$, the other experimental individual, was vigorously engaging in many

contacts and winning an increasingly greater number each day. The attention of the flock was chiefly centered about his activities. It is problematical as to what might have been the course of $X$'s later relationship to the flock, had not $RW$ so nearly monopolized the scene.

$RW$'s injections began on the thirty-fifth day of $X$'s. $RW$ had been in the lowest rank in the control period (table VI). He had engaged in numerous pecking contacts with all his flock mates but many of these were indecisive in character. In those contacts resulting in withdrawal of one or the other bird, $RW$ was the winner in about one-third of the cases. A change, similar in certain respects to that in $X$'s case, occurred in the first eight days of injection. The total

TABLE VI. *Order in peck-dominance in male flock of ring doves A as modified by injection of bird RW with male hormone. Double vertical lines enclose the injection periods*

Series I

| Doves | 8 da. | 0.5 mgm. | | | 10 da. |
| | | 8 da. | 16 da. | Total | |
|---|---|---|---|---|---|
| RW:W | 31:13 | 33:10 | 15:34 | 48:44 | 0:9 |
| RW:Z | 21:15 | 11:22 | 2:29 | 13:51 | 18:17 |
| RW:X | 0:0 | 2:1 | 2:18 | 4:19 | 0:8 |
| RW:TB | 23:12 | 15:9 | 0:39 | 15:48 | 0:16 |
| RW:FD | 12:0 | 8:6 | 10:15 | 18:21 | 9:18 |
| RW:TD | 8:1 | 6:2 | 7:32 | 13:34 | 7:11 |
| W:Z | 6:25 | 7:18 | 7:8 | 14:26 | 15:1 |
| W:X | 0:9 | 0:7 | 1:8 | 1:15 | 0:0 |
| W:TB | 4:12 | 1:33 | 0:16 | 1:49 | 0:0 |
| W:FD | 21:47 | 25:36 | 1:4 | 26:40 | 7:1 |
| W:TD | 12:1 | 3:7 | 2:19 | 5:26 | 2:1 |
| Z:X | 7:2 | 4:4 | 0:8 | 4:12 | 0:15 |
| Z:TB | 6:15 | 2:10 | 0:12 | 2:22 | 0:32 |
| Z:FD | 8:15 | 13:18 | 8:3 | 21:21 | 5:33 |
| Z:TD | 2:2 | 8:4 | 3:0 | 11:4 | 12:37 |
| X:TB | 6:8 | 3:6 | 1:6 | 4:12 | 2:0 |
| X:FD | 15:12 | 12:5 | 2:0 | 14:5 | 2:0 |
| X:TD | 2:0 | 3:0 | 4:0 | 7:0 | 3:0 |
| TB:FD | 2:27 | 1:15 | 6:1 | 7:16 | 19:0 |
| TB:TD | 10:0 | 2:1 | 8:0 | 10:1 | 9:0 |
| FD:TD | 18:0 | 2:3 | 7:0 | 9:3 | 4:3 |
| Total | 214:206 | | | 247:469 | 114:202 |
| Rank in Flock | TD(5.5) W(5) Z(3.5) X,FD,TB(2) RW(0) | W(6) TD(4) X,Z(2.5) FD,TB,RW(2) | W(6) RW(5) TD(4) Z(2.5) ED(1.5) X,TB(1) | W(6) RW(5) TD(4) Z(2.5) FD(1.5) X,TB(1) | Z(6) RW(5) TD(4) FD(3) TB(1) X,W(0) |

TABLE VI   (*Continued*)
Series II

| Doves | 8 da. | 0.5 mgm. | | | 17 da. |
| | | 8 da. | 16 da. | Total | |
|---|---|---|---|---|---|
| RW:W | 20:0 | 0:11 | 0:14 | 0:25 | 0:10 |
| RW:Z | 22:0 | 1:21 | 2:20 | 3:41 | 2:14 |
| RW:X | 1:0 | 0:5 | 0:11 | 0:16 | 0:6 |
| RW:TB | 2:1 | 2:19 | 0:12 | 2:31 | 2:9 |
| RW:FD | 9:1 | 3:33 | 14:62 | 17:95 | 65:39 |
| RW:TD | 32:0 | 4:20 | 4:34 | 8:54 | 8:17 |
| W:Z | 1:11 | 4:1 | 4:12 | 8:13 | 2:4 |
| W:X | 1:4 | 4:1 | 7:4 | 11:5 | 2:2 |
| W:TB | 0:14 | 0:0 | 0:0 | 0:0 | 0:1 |
| W:FD | 1:44 | 3:0 | 13:0 | 16:0 | 23:0 |
| W:TD | 5:33 | 7:0 | 17:11 | 24:11 | 15:5 |
| Z:X | 6:15 | 3:5 | 7:15 | 10:20 | 6:2 |
| Z:TB | 0:7 | 1:1 | 1:2 | 2:3 | 3:3 |
| Z:FD | 6:21 | 9:0 | 26:3 | 35:3 | 54:4 |
| Z:TD | 2:9 | 7:1 | 32:3 | 39:4 | 17:6 |
| X:TB | 0:0 | 0:1 | 0:0 | 0:1 | 4:0 |
| X:FD | 7:6 | 2:1 | 16:1 | 18:2 | 33:0 |
| X:TD | 4:0 | 4:2 | 23:2 | 27:4 | 14:5 |
| TB:FD | 15:0 | 21:0 | 57:8 | 78:8 | 60:8 |
| TB:TD | 14:0 | 4:0 | 2:0 | 6:0 | 12:0 |
| FD:TD | 31:5 | 9:3 | 20:15 | 29:18 | 42:34 |
| Total | 179:171 | | | 333:354 | 364:169 |
| Rank in Flock | W(6) Z(5) TD(4) FD(3) X,TB(1) RW(0) | RW(6) TD(5) FD(4) Z(2.5) X(2) TB(.5) W(0) | RW(6) TD(5) FD(4) Z(2) X,W(1) TB(0) | RW(6) TD(5) FD(4) X,Z(2) W(1) TB(0) | FD,TD,RW(5) W(2.5) X,TB(1.5) Z(.5) |

number of decision contacts in the flock decreased, although those in which *RW* participated increased. Unlike the slight increment in *X*'s case, *RW*'s proportion of successes rose from one-third to nearly three-fourths of the total winning combats. Non-decision encounters practically ceased. Increased vigor and effectiveness on *RW*'s part was quite comparable to that in the initial stages of *X*'s injections. Unlike *X*, *RW* showed no change in rank until the fourteenth day. He was then in fourth of six places. Four days later he was in second place and so remained until his treatment ceased. *RW* was still in this position when observations ended ten days later. After the three weeks' interim, in the next control period, he was once more subordinate to the entire flock, even to *X*.

In male flock *B*, *EB* alone was injected. This bird, one of the lowest ranking flock members, showed a similar trend to that in *X*'s and *RW*'s cases, an increasing proportion of winning contacts in the first eight days of injection (table VII). Also, as in the other males, the total number of flock contacts was reduced, during this period. No great advance in social status occurred. *EB* became dominant over two birds instead of one but was still in next to the lowest rank. In the midpoint of injection, *EB* was also at the midpoint in rank. Increased dosage was begun at this time but a slump in rank occurred in the succeeding eight days. In the last sixteen days, *EB* again rose in rank, this time into second place with *PB*. The total record for forty-eight days shows *EB* in middle rank.

TABLE VII. *Order in peck-dominance in male flock of ring doves B as modified by injection of bird EB with male hormone. Double vertical lines enclose the injection periods*

### Series I

| Doves | 8 da. | 0.25 mgm. | | 0.5 mgm. | | Total | 21 da. |
|---|---|---|---|---|---|---|---|
| | | 8 da. | 16 da. | 8 da. | 16 da. | | |
| EB:GB | 19:7 | 10:2 | 17:13 | 20:0 | 19:4 | 66:19 | 39:4 |
| EB:PB | 31:13 | 10:4 | 17:12 | 10:0 | 10:11 | 47:27 | 21:1 |
| EB:BH | 0:5 | 0:3 | 7:3 | 5:2 | 4:0 | 16:8 | 14:7 |
| EB:EH | 5:0 | 2:2 | 1:6 | 2:0 | 4:5 | 9:13 | 11:4 |
| EB:EW | 5:2 | 2:1 | 1:4 | 1:1 | 1:3 | 5:9 | 8:8 |
| EB:PH | 2:8 | 3:12 | 6:44 | 0:9 | 7:8 | 16:73 | 12:14 |
| GB:PB | 3:8 | 6:2 | 9:12 | 7:5 | 10:4 | 32:23 | 11:26 |
| GB:BH | 2:4 | 2:3 | 8:11 | 1:3 | 4:9 | 15:26 | 9:20 |
| GB:EH | 2:5 | 8:3 | 2:17 | 0:5 | 0:6 | 10:31 | 1:13 |
| GB:EW | 0:8 | 0:4 | 1:4 | 0:0 | 1:3 | 2:11 | 20:19 |
| GB:PH | 0:0 | 3:0 | 6:0 | 0:0 | 2:2 | 11:2 | 9:5 |
| PB:BH | 0:0 | 3:2 | 1:8 | 2:2 | 2:3 | 8:15 | 4:8 |
| PB:EH | 1:1 | 0:1 | 1:12 | 0:0 | 2:4 | 3:17 | 9:14 |
| PB:EW | 1:11 | 1:6 | 2:7 | 0:2 | 1:6 | 4:21 | 7:5 |
| PB:PH | 1:0 | 3:0 | 15:0 | 2:2 | 1:0 | 21:2 | 3:2 |
| BH:EH | 3:0 | 1:0 | 1:1 | 0:0 | 1:1 | 3:2 | 4:2 |
| BH:EW | 1:5 | 1:2 | 2:6 | 0:0 | 0:1 | 3:9 | 2:7 |
| BH:PH | 0:11 | 2:7 | 4:16 | 0:5 | 7:9 | 13:37 | 6:15 |
| EH:EW | 1:0 | 0:0 | 0:2 | 0:2 | 0:0 | 0:4 | 4:6 |
| EH:PH | 0:1 | 1:4 | 4:15 | 0:2 | 11:18 | 16:39 | 1:20 |
| EW:PH | 3:16 | 0:38 | 4:59 | 0:24 | 2:21 | 6:142 | 12:50 |
| Total | 80:105 | | | | | 306:530 | 207:250 |
| Rank in Flock | GB(5) EH(3.5) EW(3) PB(2.5) EB,BH(2) PH(1) | PB(4) EH(3.5) GB,BH(3) EB(2.5) EW,PH(2) | GB(5) PB(4) BH(3.5) EB(3) EH(2.5) PH(2) EW(1) | PB(4) GB,EH(3) BH(2.5) EW,EB(1.5) PH( .5) | GB(4.5) PB,EB(4) BH(3.5) EH,PH(1.5) EW(1) | PB(5) GB(4) EH,EB,BH(3) PH(2) EW(1) | GB,EH(4) EW(3.5) PB,BH(3) PH(2) EB(1.5) |

### Series II

| Doves | 8 da. | 0.5 mgm. | | | 17 da. |
|---|---|---|---|---|---|
| | | 8 da. | 16 da. | Total | |
| EB:GB | 8:7 | 25:3 | 59:34 | 84:37 | 63:27 |
| EB:PB | 16:7 | 15:9 | 19:28 | 34:37 | 28:8 |
| EB:BH | 1:5 | 5:3 | 14:14 | 19:17 | 14:3 |
| EB:EH | 13:9 | 3:9 | 1:18 | 4:27 | 12:17 |
| EB:EW | 4:2 | 7:5 | 4:58 | 11:63 | 20:32 |
| EB:PH | 0:3 | 2:9 | 46:42 | 48:51 | 8:28 |
| GB:PB | 12:3 | 20:14 | 28:27 | 48:41 | 13:27 |
| GB:BH | 2:2 | 0:12 | 10:33 | 10:45 | 9:30 |
| GB:EH | 5:7 | 1:2 | 2:17 | 3:19 | 3:17 |
| GB:EW | 6:5 | 6:4 | 3:22 | 9:26 | 12:52 |
| GB:PH | 4:1 | 1:9 | 23:20 | 24:29 | 11:6 |
| PB:BH | 2:1 | 0:3 | 8:5 | 8:8 | 12:6 |
| PB:EH | 5:11 | 1:3 | 1:13 | 2:16 | 5:23 |
| PB:EW | 0:2 | 4:0 | 0:17 | 4:17 | 15:40 |
| PB:PH | 3:5 | 1:9 | 23:14 | 24:23 | 8:3 |
| BH:EH | 1:1 | 1:0 | 6:8 | 7:8 | 11:13 |
| BH:EW | 0:0 | 3:0 | 0:37 | 3:37 | 10:22 |
| BH:PH | 0:4 | 1:3 | 17:29 | 18:32 | 11:24 |
| EH:EW | 0:3 | 2:0 | 1:4 | 3:4 | 11:4 |
| EH:PH | 2:13 | 0:2 | 24:43 | 24:45 | 7:19 |
| EW:PH | 1:5 | 1:4 | 33:2 | 34:6 | 3:33 |
| Total | 85:96 | | | 421:588 | 286:434 |
| Rank in Flock | PB(5) EH(3.5) EW,BH(3) GB(2.5) EB(2) PH(1) | EW(6) PB(5) GB(4) EH,EB,BH(2) PH(0) | BH(4.5) GB,PH(4) EB(3.5) PB(3) EH(2) EW(0) | GB(5) BH(4.5) EB(4) PB(3.5) EH,PH(2) EW(0) | GB,BH(5) PB,EB(3) EW,PH(2) EH(1) |

The cause of *EB*'s rise in status in the last sixteen days is not clear. It is quite as probable that a tendency to vacillate in flock relationships was operative as that increased dosage was responsible. With cessation of injections, *EB* reverted in twelve days to lowest rank and so remained until the close of observations. The pre-injection period in series II showed him still low in rank.

*Series II. Female and Male Flocks.*— The second series, undertaken as a check upon the validity of apparent modifications effected by the first, was in large part a repetition of the summer's procedure. Obviously seasonal changes were unavoidable. The location of the cages was different. Shorter periods, too, seemed advisable. In most essentials, however, the two series could be considered comparable. The flocks were the same. One bird, previously injected with testosterone propionate, from each cage was used again for the same purpose.

As has been noted, *RW* and *EB*, the experimental male birds, held practically the same social status in the original and the second series control periods. *D* was again low in rank, although not as much so as in series I.

In the second series, *D* speedily reached second rank (table II) ; in fact, she made this change in the first three days following injection, instead of in six as in series I. By the ninth day, *D* had subjugated *C* and, until the close, was alone in top rank. This includes seventeen days of post-injection observations. A fairly comparable but much condensed behavior development (table III) to that of series I was in evidence. The consummation was reached in slightly less than half the previous record. In the post-injection period, no such rapid return to pre-injection status was evident as in series I. An increased tendency to quiet perching and a decrease in courting contacts did take place, although the latter was observed in one case on the final day.

*RW* in male flock *A* attained peck dominance (table VI) over all his flock on the fifth day of injection and retained this position to the end of the second series. This was a more rapid and more complete ascendancy than that previously exhibited. Here, however, no complications with a second experimental subject obscured results. Perhaps this accounted for the more complete dominance shown. While *RW* was still in top rank in the closing days, two other birds were then sharing it with him. On the last two days he was noticeably losing in combats on the perch which previously he had kept free of intruders.

In male flock *B*, *EB* showed no such striking changes in rank (table VII) as did *RW* in flock *A*. Nevertheless, the same ranks, which had been held in similar periods in series I, were attained in the corresponding eight and sixteen day intervals. A greater contrast was found in behavior. *EB* was more active throughout series II than in series I, continuing the activity over into the post-injection period. At the end of that interval, he was still slightly above mid-rank.

## THE EFFECT OF INJECTION OF TESTOSTERONE PROPIONATE UPON THE TYPE OF DOMINANCE FOUND IN RING DOVES

An examination of the data for the birds injected with testosterone propionate shows that, in a number of cases, an apparent change in the type of dominance had occurred. In contacts with other birds, these injected individuals developed a despotic type of relationship similar to that known as a peck-right. *RW* illustrates this point. In the pre-injection period in series I (table VIII), he won twelve encounters with *TB* but lost twenty-three. In other words, *TB* was at that time peck-dominant over *RW*. In the first two weeks of injection, a similar condition persisted, so far as the total contacts are concerned. (Two weeks were used as the initial period in table VIII because it was found that the sig-

TABLE VIII. *A comparison of the tendency to develop a "Peck-right" in injected and uninjected ring doves. Double vertical lines enclose the injection periods*

| Development of a "Peck-right" | Injected | | | | | | Uninjected | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Series | Doves | 8 da. | 14 da. | 10 (or 34) da. | Day of reversal* | Series | Doves | 8 da. | 14 da. | 10 (or 34) da. |
| **1. Reversal in first two weeks** | | | | | | | | | | | |
| *a.* Peck-dominance in control period | I | RW:TB | 23:12 | 15:13 | 0:35 | 8th | — | — | — | — | — |
| | II | RW:TB | 2:1 | 2:27 | 0:4 | 2nd | — | — | — | — | — |
| *b.* "Peck-right" in control period | I | D:E | 5:0 | 8:2 | 0:67 | 12th | I | EH:EW | 1:0 | 0:2 | 0:2 |
| | I | RH:E | 6:0 | 2:12 | 0:5 | 1st | — | — | — | — | — |
| | II | RW:X | 1:0 | 0:11 | 0:5 | 3rd | — | — | — | — | — |
| | II | RW:W | 20:0 | 0:18 | 0:7 | 3rd | — | — | — | — | — |
| *c.* No contacts in control period | I | D:RH | 0:0 | 2:1 | 0:6 | 10th | — | — | — | — | — |
| | II | RH:S | 0:0 | 2:8 | 0:5 | 3rd | — | — | — | — | — |
| **2. No reversal at any time** | | | | | | | | | | | |
| *a.* No contacts in control period | I | D:T | 0:0 | 0:6 | 0:51 | — | II | RH:T | 0:0 | 0:2 | 0:5 |
| | I | D:S | 0:0 | 0:1 | 0:16 | — | II | BH:EW | 0:0 | 3:7 | 0:30 |
| | — | — | — | — | — | — | II | E:RH | 0:0 | 1:2 | 0:1 |
| *b.* "Peck-right" in control period | I | RH:T | 0:5 | 0:35 | 0:27 | — | I | C:G | 0:8 | 0:13 | 0:25 |
| | II | D:G | 0:6 | 1:40 | 0:41 | — | II | C:S | 0:14 | 0:17 | 0:14 |
| | II | D:E | 0:3 | 1:17 | 0:31 | — | II | TD:TB | 0:14 | 0:5 | 0:1 |
| | — | — | — | — | — | — | II | PB:EW | 0:2 | 4:11 | 0:6 |
| | — | — | — | — | — | — | II | PB:EH | 5:11 | 2:12 | 0:4 |
| | — | — | — | — | — | — | II | G:T | 1:2 | 0:3 | 0:24 |
| | — | — | — | — | — | — | I | TD:X | 3:8 | 2:5 | 0:7 |

\* The day of reversal refers to the day in the first two weeks of injection on which the treated bird assumed complete dominance.

nificant changes in peck-order, in all cases, occurred in fourteen days or less.) On the eighth day in this two weeks' period *TB* ceased to win any combats. For the remainder of the injection period, *RW* won in all contacts. A reversal in dominance occurred and a "peck-right" relationship became established. *RW* duplicated the essential features of this sequence in series II.

A second situation in which a peck-right type of dominance appeared also involved a reversal. In this case, however, the injected birds were completely submissive in the pre-injection period. In series I, *D* had lost in five contacts with *E* before injections began. In the first two weeks of injection she lost in eight contacts but won two. In the remainder of the injection period *D* was always the winner. In the same series *RH,* and in series II, *RW,* the latter in two cases, showed reversal, and subsequent complete dominance, similar to that in *D*'s case. On the other hand, in the contact pair, *EH* and *EW* in series I, the same kind of a development occurred although

neither bird had been treated with the hormone.

A reversal occurred in a third combination of contacts. *D* in series I and *RH* in series II, in relation to uninjected birds, *RH* and *S,* respectively, had no contacts in the pre-injection periods. After a few contacts, the first two weeks of injections, in which one or the other might withdraw, the injected birds became established as despots. No similar cases appeared in pairs of untreated individuals.

A number of cases, in which no reversal occurred, showed a more or less gradual development of a peck-right type of dominance. In series I, *D* had no contacts with *T* or *E* preceding injection. Following injection, numerous combats occurred. *D* won all. In series II, three similar cases were recorded in pairs in which none of the birds had been treated. Apparently, such cases occur more or less independent of injection with male hormone. Other cases in which reversal did not occur were noted. In these the injected birds were dominant in both the

pre-injection and injection periods. Eight similar cases, in point of time and sequence of developments, occurred in pairs in which no injected birds were present. This fact supports the conclusion that consistency in dominance, which eventually approaches a peck-right, is not dependent upon injection with testosterone propionate. However, there are strong indications in the situation as a whole that treatment with this androgen causes a decided trend away from the looser peck-dominance toward the more stable peck-right type of social organization.

## DISCUSSION

The data from observations in this investigation on the effects of testosterone propionate, in both series, in pre-injection, injection, and post-injection periods, show the usual alignment in hierarchies of the peck-dominant type (tables II, IV, V, VI, and VII). Moreover, the data support Riddle's assumption (Whitman, '19) that combats in ring doves in either sex probably depend upon varying degrees of maleness. In the case of both sexes, in all flocks, the same general trend is apparent so far as the experimental birds are concerned (table IX). These birds

TABLE IX. *Number of birds in each ring dove flock over which peck-dominance was held by individuals treated with male hormone. One point is allowed for complete peck-dominance; five-tenths points for shared rank*

| Dove | Series I | | | Series II | | |
|---|---|---|---|---|---|---|
| | Pre-injection | In-jection | Post-injection | Pre-injection | In-jection | Post-injection |
| ♂ X | 1.5 | 4.0 | 1.0 | 1.5 | — | — |
| ♂ RW | 0.0 | 5.0 | 5.0 | 0.0 | 6.0 | 5.0 |
| ♂ EB | 1.5 | 3.0 | 0.0 | 1.0 | 4.0 | 3.5 |
| ♀ D | 0.5 | 5.5 | 4.0 | 1.5 | 6.0 | 6.0 |
| ♀ RH | 0.5 | 5.5 | 5.5 | 1.5 | — | — |
| Mean | 0.8 | 4.6 | 3.1 | 1.1 | 5.3 | 4.8 |

each advanced in flock rank in a more or less marked degree and maintained the new status with considerable consistency, at least so long as injections continued.

The change in female flock position was consistently quite marked, that in males in most cases less so. Not only was a general trend characteristic in relation to rank, but also in behavior. More activity was shown in the winning contacts on the part of the experimental subjects. In females increased and livelier courting behavior of a male character developed. The observations as a whole lead to the conclusion that an elevation in social rank in ring doves is correlated with augmented aggressiveness in behavior. Apparently such behavior is characteristically male.

Ascendancy in each of the experimental birds appeared in a clearly marked degree after from five to fourteen days of injection with testosterone propionate. In the second series it developed more rapidly in two cases, D's and RW's, than in the first; in EB's, less so. The decline toward submissiveness, following cessation of injection, was not rapid in most of the cases. X dropped quickly, but as has been noted, his case was complicated by RW's. EB in flock B showed a similar tendency in series I but the reverse in series II. It may be in series I that the treatment in X's and EB's cases, in late summer, had postponed molting beyond that of their flock mates. After injection ceased and molting set in, the lowered vitality of these birds may then have operated against them, offsetting the hold-over effect of hormonal treatment on pugnacity.

Allee and co-workers ('39) found in hens that "higher position once won was retained." In ring doves, with two exceptions, the birds injected with testosterone propionate, after once attaining a higher status, maintained this rank while injections were still continuing. Consistency in the maintenance of the higher status was not as marked in these birds as in hens, although there was some approach toward such stability. As previously noted, X in male flock A, series I, held a lower rank in the last sixteen days than at any time following his initial rise. EB's status in series I under-

went a temporary slump immediately following the midpoint in injection. *EB*, unlike *X*, recovered his previous status when the dosage was increased. Moreover, he improved it. It may be that as high consistency in maintenance of rank is not to be expected of birds whose social organization is peck-dominant in type as of those with a definite peck-order.

While the ring doves, during injections, showed a fixity in newly acquired status somewhat approaching that found in hens, with cessation of treatment the situation was not parallel. In the first series, as previously noted, both *X* and *EB* rather abruptly resumed a lower status. That all such doves may return to the low ranks in which they were originally observed is indicated. The data obtained in the control period for series II, thirty-nine days in two cases and fifty days in three, following cessation of treatment, showed all five experimental birds in ranks corresponding to those in the original pre-injection period. The time element seems an important one. Physiological changes probably occur. Memory, too, may play an important rôle.

The social structure of the entire flock appeared to acquire greater stability during the latter part of the injection periods. Frequently ring doves high in rank at any given time are found to be consistently so at all times. An inspection of tables II, VI, and VII will show that female *C* and males *TB* and *GB* are birds of this type. Perhaps with the advancement of an additional bird, under conditions which seem to develop stability in the bird itself, the flexibility of the group is lessened. At any rate, during a period of seventeen days, late in the first series' injection period, no change occurred in the hierarchy in male flock *A*. Each rank, too, was occupied by a single bird. This flock structure broke up only as injections of the second member, *RW*, were initiated. In male flock *B*, no change in relationship occurred after the twenty-third day, that is, during the latter half of the period of treatment. In this case, a linear flock

order, nearly as complete as in flock *A*, was observed. In only one case was there more than one bird in a rank. In that there were two. An implication of this tendency toward increased social stability, which was observed when a single bird was treated with male hormone, together with the fact that frequently birds high in rank are consistently so, may be that in birds showing the peck-dominant type of social order, the hormonal balance is less stable than in those where the peck-right is found.

That the explanation of the increased stability observed may lie in the expression of territorialism, rather than in any new development, is altogether possible. Territory is, without question, a factor in the organization of many flocks, even in highly domesicated birds such as pigeons and doves. Taylor ('32) in referring to this matter says that "when the intruder has slipped into his own place his neighbors pay no more attention to him; but if he is out and some other bird comes into place . . . a neighboring bird will drive out the invader promptly and emphatically." Even in the limited confines of the cages and in the homosexual flocks used in this investigation, there were a number of evidences of such behavior. In male flock *A* in the second series, the experimental bird appropriated one perch and usually maintained it against all others. If he left it and a second bird sought to occupy it, he sometimes ignored the fact, particularly when feeding. Certain remaining birds would chase the intruder away as if disturbed by the presence of other than the customary resident. Flock *A* did become quite strictly territorialized in the same period in which the flock structure was notably stable. Still the evidence that territorialism fully explained increase in flock stability is inconclusive. The experimental birds, with the exception of the one in flock *A* in series II, became more mobile and less confined to a particular location as injections continued.

In ring doves, behavior changes appeared, following the initiation of injec-

tions of testosterone propionate, with greater expedition than the observed modification in social status. The latter appeared in definite form in from five days to two weeks. In males, a decrease in the number of observed pecking contacts appeared to follow the marked change from submissive to aggressive behavior on the part of the experimental bird in the flock. In females the initial appearance of the stages of the gamut of male courting conduct preceded in each case the first observable modifications in social status. $D$'s first bowing-coo preceded by one day her first advance in rank. $RH$ began frequently and vigorously performing this same act on the second day, although observed in it but once before treatment. The fact that behavior changes preceded changes in social position, agrees with the observations in flocks of hens (Allee and others, '39).

The data from the second series of injections show no significant differences from those obtained in the first series. It appears that the same birds, in relation to the same flocks, after an extended recess in experimental treatment, react very similarly, both in relation to the social hierarchy and in individual behavior. The female response in both behavior and ascendency was more accented than that of the males, but both females and males reacted more readily in the second than in the original series. This increment in efficiency suggests that some holdover from the first series, it may be both psychological and physiological, is in operation. That results in both series show similarity and that they parallel results in flocks of other birds as widely different as chickens and canaries, appears to support the theory that male sex hormone is an important factor in flock organization of birds.

Cases in which a peck-right form of relationship develops between members of a ring dove pair are not uncommon. The data in series I and series II (Table VIII) indicate that such developments may appear in both injected and uninjected indi-

viduals in the same intervals of time. Eight cases, involving reversal following injection, developed into a situation comparable to a peck-right. A single case of a similar type appeared among the uninjected birds. Apparently in the remainder of all cases in which a shift in balance of power was taking place, peck-dominance prevailed. Five cases, in which no reversal occurred, but in which the injected bird was the dominant one, developed, or maintained throughout, a peck-right type of dominance. Ten such cases were recorded for doves which were not injected. Evidently such cases are far from unique. On the other hand, two observations support the conclusion that the frequency of development of the peck-right type of dominance is greater in injected birds than in untreated ones. In the first place, a shift in dominance in untreated birds rarely resulted in the peck-right condition. In treated birds, a number of such developments followed the beginning of injection. In the second place, a greater percentage of possible contact pairs, in which one bird was injected, developed a peck-right type of dominance than was the case in the others. The possible contact pairs of the injected individuals were forty-eight (five birds in series I and three in series II, with six possible contact pairings each). This is in contrast with 170 possible pairings (204, if injected birds are included) with uninjected birds. The records show nine cases, or 18.7 per cent, of the possible contact pairings in injected birds, with a peck-right type of dominance following two weeks of injection and persisting so long as injections continued. In possible pairings, of uninjected birds, 6.4 per cent show a similar sequence of development. The evidence suggests that injection of ring doves with testosterone propionate is accompanied by an increase in development of a peck-right type of dominance as contrasted with the usual peck-dominant social order found in these birds.

## SUMMARY

1. Administration of testosterone propionate to a low ranking, submissive member of a caged flock of ring doves of either sex, in all cases, resulted in advance in social status and, in all but two partial exceptions, in a maintenance of this position throughout an extended period of injection.

2. Repetition of the procedure, after an interval of weeks, using the same flocks and three of the same individuals for the experimental treatment, produced results paralleling those of the original series.

3. Behavior changes occurred in the injected individuals of both sexes. Both showed increase in vigor and augmented effectiveness in combat. Male sex behavior characteristics in a cumulative, progressive series appeared in hitherto passive females.

4. Peck-dominance rather than peck-right is the rule in caged flocks of ring doves. Occasional cases of dominance, similar to a peck-right, appear in dove flocks. The injection of flock members with testosterone propionate is followed by an increased development of a peck-right type of dominance, not explained by the ordinary sequence of events among uninjected flock members.

5. A modification in the social hierarchy of the ring dove flock can be induced by treatment of one of its members with an androgen. The results seem to support the conclusion that, as in chickens and canaries, one approach has been found to a better understanding of the physiological processes which underlie the social organization in birds.

6. Treatment with male hormone augmented aggressiveness in both female and male ring doves. This investigation, therefore, experimentally confirms Riddle's postulation, made two decades ago, that combats in either sex of these birds are probably due to varying degrees of maleness.

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# A TROPICAL HAMMOCK ON THE MIAMI (FLORIDA) LIMESTONE

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The vegetation of southern Florida has been much neglected in serious research, although there have been numerous sketches of the country written by early travelers who concentrated on the aspects of the coastal areas accessible to visitors. Harshberger ('11, '14) has given rather general treatments of the whole southern area which are exceedingly well done considering the lack of means of travel in early times. Harper ('27) has also covered southern Florida in one of the annual reports of the Florida State Geological Survey. Harper's work is a good ecological description of the whole region of Florida south of Tampa on the west coast, and Melbourne on the east coast. It was written after new means of travel had been developed in the marshy regions of southern Florida, and he showed exceedingly keen judgment in working over this extensive region. However, a report of this sort covering such a diverse area cannot give proper emphasis to the various smaller but very interesting elements of the vegetation.

Other literature of the region deals with collections of newly discovered plants or popular descriptions of the tropical regions of southern flora. Ames ('04) describes many of our epiphytic orchids found in hammocks. Chapman (1878) noted many new plants as he was preparing his volume on the southern flora. Dodge (1894) and Simpson ('20, '23) have written excellent descriptions of the area from naturalists' point of view, and given information on the appearance of the country before the advent of civilization. Small ('07, '16) has written much on the region and has explored it botanically over a period of 35 years, but in all his reports there is little information of a definite character aside from lists of plants collected.

The flora of southern Florida is rapidly being destroyed by advancing civilization, drainage (see last title of Literature Cited) and burning—a result of drainage. True, there have always been fires sweeping the area at various times but none like the fires of the last few years and especially of 1939.

## LOCATION OF HAMMOCK

Southwest of Miami on the porous limestone ridge (fig. 1) running parallel with the coast [Miami limestone (Harper, '27)] there are numerous islands of vegetation known as tropical hammocks. These particular hammocks are composed of a dense growth of hardwood trees mainly of tropical origin. They are rapidly being cut down and destroyed to make way for cultivated areas, or if they escape complete destruction they are being seriously burned into from constant fires in the adjacent pinelands. This paper deals with one of the larger of these hammocks that is uncomfortably close to cultivated land and will probably be destroyed in the not too distant future. There is talk at the present time of running a road directly through the center of the hammock to connect other roads already completed to the west and east.

Castellow Hammock is situated about 20 miles southwest of Miami, a half mile north of the settlement known as Silver Palms (S.E. quarter of section 17, township 56, range 39 east). The name comes from the original homesteader, James S. Castellow, who received his homestead deed in September 1905 after originally settling there in 1899. Mr. Castellow's homestead included the southern part of the hammock, the northern part being on the Ross homestead. Newton Road runs along the eastern edge of Castellow hammock and bisects Ross

Fig. 1. Miami limestone. Area outside of hammock with vegetation burned away showing porous nature of the substrate.

hammock (fig. 2). In literature the name Castellow has been recorded as Costello, but the original deed gives the correct name. At present Castellow hammock occupies about 38.3 acres although originally it was slightly larger.

Hurricanes have felled numerous of the larger trees, and fires are annually burning into the edges. A hurricane in 1935 swept across the area and did some damage to Castellow Hammock but Ross Hammock, only a few hundred yards to the northeast across a strip of pineland, was very badly torn apart. Ross Hammock is now a tangled mass of fallen trees, and vines cover the dead trees making passage all but impossible.

Although the name Castellow Hammock is generally known in this region and appears on many herbarium sheets as a locality record, there is a surprising absence of the mention of this hammock in literature. Safford ('19) has a map with many early landmarks and locates

Castellow Hammock. In all of Small's writings I can find only one reference to Castellow Hammock (Small, '16) and that is merely a remark that he visited the hammock three times on one trip.

The term hammock is applied to several different types of plant associations. The term as here used corresponds to the definition given by Harper ('05) in a paper in which he discusses the derivation of the word and its various corruptions. In a later paper Harper ('11) uses the term hammock as synonymous with climax. The term hammock as used in northern Florida by Thone ('27) also refers to the climax type of vegetation and does not give the idea of an island of vegetation.

VEGETATION OF CASTELLOW HAMMOCK

Castellow Hammock seems to be typical of the many tropical hammocks that occur on the Miami Pineland. It is probably at the present time in a better state of preservation than most of the other hammocks and contains many large sinks which are not always present in these hammocks. The aspects of this island type of vegetation can easily be seen in the aerial photograph (fig. 2) which discloses Ross and Castellow Hammocks as distinct units surrounded by pinelands.

From above, tropical hammocks have a light gray-green border which on investigation proves to be caused by the foliage of live oaks (*Quercus virginiana*). Large trees of live oak are found occasionally in the interior of the hammocks and represent relics of earlier stages in succession, but around the outer edge one may find oaks of all ages and sizes. This would tend to prove Bessey's ('11) explanation as to the genesis of hammocks. It might be well to state here that there are several different types of hammocks present in south Florida, and the oak rims are present only in the tropical hammocks found on the Miami Pineland and its extension into Long Pine Key. The marginal area of these tropical hammocks (fig. 3) tends to be shrubby, with vines

and shrubs making an almost impossible barrier to the interior. The central part of the hammock, while it still has the shrubby undergrowth, does not retain the impenetrable nature of the margin. The large trees which are rather evenly scat-

tered throughout the interior of the hammock and the smaller trees and shrubs intermediate form a solid canopy. Where there are breaks in this canopy, due to fallen trees, a dense growth of sword fern several feet in height takes possession.
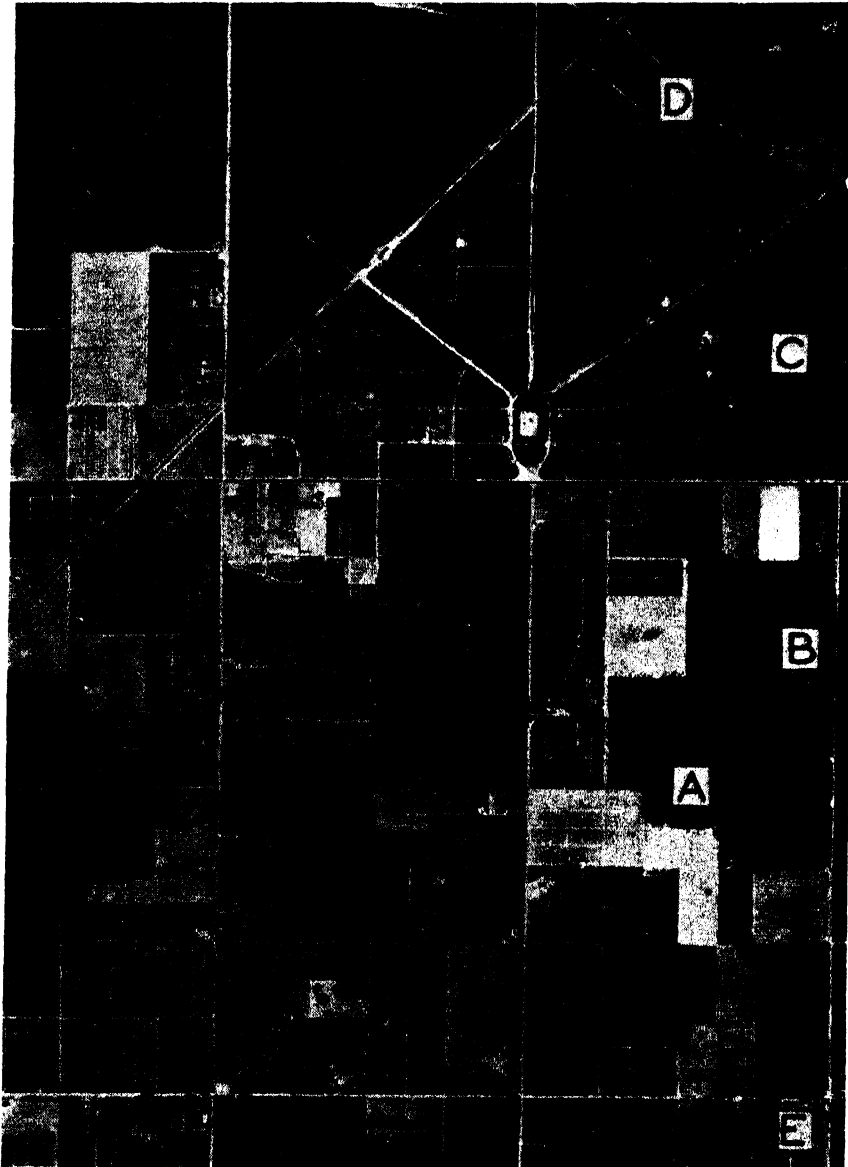


Fig. 2. Aerial view of region around Castellow Hammock. *A* is Castellow Hammock; *B*, Ross Hammock bisected by Newton Road; *C*, area of pineland showing the scattered pines; *D*, slough in pineland running back from coastal areas; *E*, settlement of Silver Palms at intersection of Newton Road and Silver Palm Drive. The cultivated areas of evenly spaced plants are citrus groves. (Photo, courtesy of Agricultural Adjustment Administration.)

FIG. 3. Castellow Hammock from the pine-lands. *Pinus caribaea* and *Serenoa repens* in the foreground the two main plants of the Miami Pineland area. The margin of the ham-mock is in the background. The tallest trees in the hammock are *Lysiloma bahamensis*.

## Flora of sink holes

Scattered through the interior of the hammock are sink holes of various sizes. They vary in depth to ten feet, but most of the larger sinks and many of the smaller are between eight and ten feet deep. Some sinks a foot in diameter may be ten feet deep. In these sinks are beau-tiful displays of ferns and mosses.

The ferns are mostly typical of the West Indies and are found only in the depths of the hammock on the moist walls of the sinks (fig. 4, 5). During the rainy season the sinks have water in the bot-tom; however, the water soon recedes in the dry season and leaves a moist humus in which *Proserpinaca palustris* grows. The only *Annona glabra* found in this hammock occurs in one of the larger sinks.

List of ferns found in sinks.—*Adian-tum tenerum, Asplenium verecundum, Tectaria heracleifolia, Tectaria minima, Dryopteris ampla, Dryopteris reptans, Trichomanes punctatum, Trichomanes kraussii.*

## Belt transect

To get a clear idea of the composition of this hammock, a belt-transect was worked out. The transect was two me-ters wide and 150 meters long running from the edge of the hammock to a point past the center. The plants noted were living plants occurring within or touching on the two meter strip. Epiphytes and vines in the canopy but not rooted in the area were not included. The labor in-volved in running a transect through the hammock was great, but worthwhile re-sults were obtained indicating a definite marginal composition and a tropical in-terior (fig. 6).

The marginal and the interior natures of the composition of this hammock showed up well when the trees were plotted as to their occurrence in each me-ter of the transect. The margin of the hammock was a zone about 15 meters in width. Here the live oaks (*Quercus vir-giniana*) were the large trees, and other marginal plants mingled with waifs from the pineland.

Plants typical of the marginal area.— *Quercus virginiana, Pinus caribaea, Sabal palmetto, Serenoa repens, Metopium toxi-ferum, Tetrazygia bicolor, Lantana de-pressa, Chiococca pinetorum, Rhabdadenia corallicola, Rhus leucantha, Ilex cassine.* Fifteen meters from the outside, however, the marginal plants had dropped out and the plants typical of the interior of these tropical hammocks had appeared.

Trees typical of the interior of the hammock.—*Nectandra coriacea, Lauro-cerasus myrtifolia, Coccolobis laurifolia, Lysiloma bahamensis, Elaphrium sima-ruba, Simarouba glauca, Exothea panicu-lata, Ilex krugiana, Ficus aurea, Dipholis salicifolia, Sideroxylon foetidissimum, Icacorea paniculata, Chrysophyllum oli-vaeforme, Krugiodendron ferreum.*

Total population of the hammock tree species in percentages.—*Nectandra cori-acea,* 26; *Laurocerasus myrtifolia,* 15; *Coccolobis laurifolia,* 15; *Lysiloma ba-hamensis,* 8; *Elaphrium simaruba,* 5;

Fɪɢ. 4. Wall of limestone sink in Castellow Hammock. *A, Dryopteris reptans; B, Tectaria minima; C, Trichomanes punctatum.*



Fɪɢ. 5. Rock in bottom of limestone sink. *A, `Trichomanes punctatum; B, Campyloneurum phyllitidis; C, Nephrolepis exaltata; D, Asplenium verecundum.*

FIG. 6. Interior of Castellow Hammock showing dense nature of hammock vegetation. Taken on Belt-transect and showing the line and students working on transect.

*Simarouba glauca*, 5. Each of the rest of the tree species had less than 5 per cent of the total plant population. In the marginal zone *Quercus virginiana* accounted for 15 per cent of the tree population.

## RELATIONSHIP OF HAMMOCK FLORA

Grisebach (1865) states that the flora of southern Florida shows more affinities with the North American flora than with the West Indian flora. Brendel (1874) criticizes this point of view and shows that most of Grisebach's work was based on the incomplete information available at the time. Brendel points out many of the similarities between the flora of south Florida and the West Indies and gives lists of plants common to the two regions. DePourtales (1877) further emphasizes that the two regions have many plants in common but he deals mainly with the keys off the coast of south Florida.

In making up the list of plants found in Castellow hammock it was deemed worth while noting their distribution not

only in continental United States but also their occurrence in the West Indies. With this information it is clear that at least the flora of this tropical hammock shows definite affinities with the West Indian flora. This would also hold true for the other hammocks in this region.

Of the 128 species found in the hammock 62 per cent are found only in southern Florida in the United States. Only 22 per cent occur outside of the northern reaches of the state and those, in many cases, only into south Georgia and other states adjacent to Florida. Five per cent are endemic to south Florida while 82 per cent of the species found in this hammock are also found in the West Indies.

## SUMMARY

1. A brief review of the previous work on south Florida ecology is given.

2. Castellow Hammock on the Miami Pineland is located and described.

3. The margin and interior of the hammock are discussed and lists of plants common to the areas given.

4. Sink holes in the hammock have many fern species peculiar to Miami hammocks; these are listed.

5. A belt transect gave information as to the percentage of the various species found in this hammock.

6. A list of plants found in Castellow Hammock is given with a supplementary list of other species found in nearby hammocks but not found in Castellow.

7. The relationship of the species in this hammock is discussed in relationship to the rest of the continental north America and the West Indies.

### List of Plants Found in Castellow Hammock [1]

Cycadaceae
    *Zamia integrifolia* Ait. — Fla.
Pinaceae
    *Pinus caribaea* Morelet — Pen. Fla. — W. I.
Poaceae
    *Lasiacis divaricata* (L.) A. Hitchc. — S. Fla. — W. I.
Arecaceae
    *Sabal palmetto* (Walt.) Lodd. — S. U. S. — W. I.
    *Coccothrinax argentea* (Lodd.) Sarg. — S. Fla. — W. I.
    *Serenoa repens* (Bartr.) Small — S. U. S.
Bromeliaceae
    *Dendropogon usneoides* (L.) Raf. — S. U. S. — W. I.
    *Diaphoranthema recurvata* (L.) Beer. — S. U. S. — W. I.
    *Tillandsia tenuifolia* L. — Fla. — W. I.
    *Tillandsia balbisiana* Schult. — S. Fla. — W. I.
    *Tillandsia circinata* Schlecht. — S. Fla. — W. I.
    *Tillandsia utriculata* L. — Fla. — W. I.
    *Catopsis berteroniana* (Schult.) Mez. — S. Fla. — W. I.
Orchidaceae
    *Habenella odontopetala* (Reichenb. f.) Small — Pen. Fla. — W. I.
    *Physurus sagraeanus* A. Rich. — S. Fla. — W. I.
    *Amphiglottis difformis* (Jacq.) Britton — S. Fla. — W. I.
    *Amphiglottis nocturna* (L.) Britton — S. Fla. — W. I.
    *Encyclia tampensis* (Lindl.) Small — Pen. Fla. — W. I.
    *Anacheilium cochleatum* (L.) Hoffmg. — Pen. Fla. — W. I.
    *Polystachya minuta* (Aubl.) Britton — S. Fla. — W. I.
    *Bletia purpurea.* (Lam.) DC. — Pen. Fla. — W. I.
    *Cyrtopodium punctatum* (L.) Lindl. — S. Fla. — W. I.
    *Platypus altus* (L.) Small — S. Fla. — W. I.
Piperaceae
    *Rhynchophorum obtusifolium* (L.) Small — S. Fla. — W. I.
Myricaceae
    *Cerothamnus ceriferus* (L.) Small — S. U. S. — W. I.
Fagaceae
    *Quercus virginiana* Mill. — S. U. S. — W. I.
    *Quercus pumila* Walt. — S. U. S.
Artocarpaceae
    *Morus rubra* L. — E. U. S.
    *Ficus aurea* Nutt. — Pen. Fla. — W. I.
    *Ficus brevifolia* Nutt. — Pen. Fla. — W. I.
Ulmaceae
    *Celtis mississippiensis* Bosc. — E. U. S. — W. I.
    *Trema floridana* Britton — S. Fla.
Polygonaceae
    *Coccolobis laurifolia* Jacq. — Pen. Fla. — W. I.
Phytolaccaceae
    *Rivina humilis* L. — S. U. S. — W. I.
    *Phytolacca americana* L. — E. U. S.
Pisoniaceae
    *Pisonia aculeata* L. — S. Fla. — W. I.
Annonaceae
    *Annona glabra* L. — S. Fla. — W. I.
Amygdalaceae
    *Laurocerasus myrtifolia* (L.) Britton — S. Fla. — W. I.
Mimosaceae
    *Lysiloma bahamensis* Benth. — S. Fla. — W. I.
Cassiaceae
    *Ditremexa ligustrina* (L.) Britton & Rose — Pen. Fla. — W. I.
Fabaceae
    *Crotalaria pumila* Ortega — Pen. Fla. — W. I.
    *Petalostemon carneus* Michx. — S. U. S.
    *Ichthyomethia piscipula* (L.) A. Hitchc. — S. Fla. — W. I.
    *Leucopterum parvifolium* (DC.) Small — S. Fla. — W. I.
    *Erythrina arborea* (Chapm.) Small — S. Fla.

[1] The nomenclature used in this paper is that of Small's *Manual of the Southeastern Flora* (1933) for seed plants and Small's *Ferns of Florida* (1931) for the Pteridophytes. The nomenclature used in these manuals is admittedly not the best, but for the sake of uniformity and reference these names have been rigidly adhered to. Following each plant name is its general distribution in the United States and its occurrence in the West Indies. Pen. Fla. indicates peninsular Florida; S. Fla. represents the very southern tropical tip of the peninsula; W. I. indicates West Indies.

Rutaceae
    *Zanthoxylum fagara* (L.) Sarg.      S. Fla.      W. I.
    *Amyris elemifera* L.      S. Fla.      W. I.
Simaroubaceae
    *Simarouba glauca* DC.      S. Fla.      W. I.
    *Alvaradoa amorphoides* Liebm.      S. Fla.      W. I.
Burseraceae
    *Elaphrium simaruba* (L.) Rose      S. Fla.      W. I.
Euphorbiaceae
    *Drypetes lateriflora* (Sw.) Krug & Urban      S. Fla.      W. I.
    *Tragia saxicola* Small      Pen. Fla.
    *Gymanthes lucida* Sw.      Pen. Fla.      W. I.
    *Bivonea stimulosa* (Michx.) Raf.      S. U. S.
Spondiaceae
    *Metopium toxiferum* (L.) Krug & Urban      S. Fla.      W. I.
    *Toxicodendron radicans* (L.) Kuntze      E. U. S.      W. I.
    *Rhus leucantha* Jacq.      S. Fla.      W. I.
Aquifoliaceae
    *Ilex krugiana* Loesener      S. Fla.
    *Ilex cassine* L.      S. U. S.      W. I.
Celastraceae
    *Rhacoma ilicifolia* (Poir.) Trelease      S. Fla.      W. I.
Sapindaceae
    *Exothea paniculata* (Juss.) Radlk.      Pen. Fla.      W. I.
Frangulaceae
    *Krugiodendron ferreum* (Vahl) Urban      S. Fla.      W. I.
    *Colubrina colubrina* (Jacq.) Millsp.      S. Fla.      W. I.
    *Gouania lupuloides* (L.) Urban      S. Fla.      W. I.
Vitaceae
    *Vitis coriacea* Shuttlw.      Pen. Fla.      W. I.
    *Muscadinia munsoniana* (Simpson) Small      Fla.      W. I.
    *Cissus sicyoides* L.      S. Fla.      W. I.
    *Ampelopsis arborea* (L.) Rusby      S. U. S.      W. I.
    *Parthenocissus quinquefolia* (L.) Planch.      E. U. S.      W. I.
Turneraceae
    *Piriqueta tomentosa* H.B.K.      S. Fla.
Papayaceae
    *Carica papaya* L.      Pen. Fla.      W. I.
Passifloraceae
    *Passiflora sexflora* Juss.      S. Fla.      W. I.
    *Passiflora pallens* Poepp.      S. Fla.      W. I.
    *Passiflora pallida* L.      Pen. Fla.      W. I.
Lauraceae
    *Nectandra coriacea* (Sw.) Griseb.      Pen. Fla.      W. I.
Melastomaceae
    *Tetrazygia bicolor* (Mill.) Cogn.      S. Fla.      W. I.
Myrtaceae
    *Calyptranthes pallens* (Poir.) Griseb.      S. Fla.      W. I.
    *Mosiera longipes* (Berg.) Small      S. Fla.      W. I.
Gunneraceae
    *Proserpinaca palustris* L.      E. U. S.
Ardisiaceae
    *Rapanea guayanensis* Aubl.      Pen. Fla.      W. I.
    *Icacorea paniculata* (Nutt.) Sudw.      S. Fla.      W. I.
Sapotaceae
    *Chrysophyllum olivaeforme* L.      S. Fla.      W. I.
    *Sideroxylon foetidissimum* Jacq.      S. Fla.      W. I.
    *Dipholis salicifolia* (L.) A. DC.      S. Fla.      W. I.
Gentianaceae
    *Leiphaimos parasitica* Schlecht & Cham.      S. Fla.      W. I.
Apocynaceae
    *Rhabdadenia corallicola* Small      S. Fla.
Asclepiadaceae
    *Asclepiodora viridis* (Walt.) A. Gray      S. U. S.
    *Amphistelma scoparia* (Nutt.) Small      S. U. S.
Solanaceae
    *Solanum verbascifolium* L.      Pen. Fla.      W. I.
Heliotropiaceae
    *Tournefortia hirsutissima* L.      S. Fla.      W. I.
Verbenaceae
    *Goniostachyum citrosum* Small      S. Fla.      W. I.
    *Lantana depressa* Small      S. Fla.

| | | |
|---|---|---|
| *Lantana involucrata* L. | S. Fla. | W. I. |
| *Citharexylum fruticosum* L. | S. Fla. | W. I. |
| *Callicarpa americana* L. | S. U. S. | |
| Rhinanthaceae | | |
| *Bramia monnieri* (L.) Pennell | S. U. S. | |
| *Buchnera elongata* Sw. | S. Fla. | W. I. |
| Olacaceae | | |
| *Schoepfia chrysophylloides* (A. Rich.) Planch | Pen. Fla. | W. I. |
| Rubiaceae | | |
| *Randia aculeata* L. | S. Fla. | W. I. |
| *Hamelia patens* Jacq. | S. Fla. | W. I. |
| *Guettarda scabra* Vent. | S. Fla. | W. I. |
| *Chiococca alba* (L.) A. Hitchc. | Pen. Fla. | W. I. |
| *Chiococca pinetorum* Britton | S. Fla. | W. I. |
| *Psychotria nervosa* Sw. | S. Fla. | W. I. |
| *Psychotria sulzneri* Small | Pen. Fla. | W. I. |
| *Morinda roioc* L. | Pen. Fla. | |
| *Diodia virginiana* L. | S. U. S. | |
| Carduaceae | | |
| *Eupatorium villosum* Sw. | S. Fla. | W. I. |
| *Aster adnatus* Nutt. | S. U. S. | |
| *Aster concolor* L. | E. U. S. | |
| *Phaethusa laciniata* (Poir.) Small | S. U. S. | |
| Hymenophyllaceae | | |
| *Trichomanes punctatum* Poir. | S. Fla. | W. I. |
| *Trichomanes kraussii* Hook. & Grev. | S. Fla. | W. I. |
| Schizaeaceae | | |
| *Anemia adiantifolia* (L.) Sw. | S. Fla. | W. I. |
| Polypodiaceae | | |
| *Polypodium polypodioides* (L.) A. Hitchc. | S. U. S. | W. I. |
| *Phlebodium aureum* (L.) R. Br. | Pen. Fla. | W. I. |
| *Campyloneurum phyllitidis* (L.) Presl. | Pen. Fla. | W. I. |
| *Vittaria lineata* (L.) J. E. Smith | Pen. Fla. | W. I. |
| *Pycnodoria pinetorum* Small | S. Fla. | W. I. |
| *Pteris caudata* L. | Pen. Fla. | W. I. |
| *Adiantum tenerum* Sw. | Fla. | W. I. |
| *Asplenium verecundum* Chapm. | Pen. Fla. | W. I. |
| *Tectaria minima* Underw. | S. Fla. | W. I. |
| *Tectaria heracleifolia* (Willd.) Underw. | Pen. Fla. | W. I. |
| *Dryopteris ampla* (H. & B.) Kuntze | S. Fla. | W. I. |
| *Dryopteris normalis* C. Chr. | S. U. S. | W. I. |
| *Dryopteris reptans* (J. F. Gmel.) C. Chr. | Fla. | W. I. |
| *Nephrolepis exaltata* (L.) Schott | Pen. Fla. | W. I. |

*List of plants found in nearby hammocks but not specifically noted in Castellow:*

| | | |
|---|---|---|
| Salicaceae | | |
| *Salix amphibia* Small | Pen. Fla. | |
| Mimosaceae | | |
| *Pithecolobium guadelupense* Chapm. | S. Fla. | W. I. |
| Simaroubaceae | | |
| *Picramnia pentandra* Sw. | S. Fla. | W. I. |
| Lauraceae | | |
| *Tamala borbonia* (L.) Raf. | S. U. S. | |
| Myrtaceae | | |
| *Eugenia buxifolia* (Sw.) Willd. | S. Fla. | W. I. |
| *Eugenia axillaris* (Sw.) Willd. | S. Fla. | W. I. |
| *Eugenia confusa* DC. | S. Fla. | W. I. |
| Ebenaceae | | |
| *Diospyros virginiana* L. | E. U. S. | |
| Oleaceae | | |
| *Forestiera porulosa* (Michx.) Poir. | S. Fla. | W. I. |
| Acanthaceae | | |
| *Ruellia parviflora* (Nees) Britton | E. U. S. | |
| Olacaceae | | |
| *Ximenia americana* L. | Pen. Fla. | W. I. |

*Plants found in Castellow Hammock according to families, genera and species:*

| | Families | Genera | Species |
|---|---|---|---|
| Pteridophytes | 3 | 13 | 17 |
| Spermatophytes | 48 | 98 | 111 |
| Totals | 51 | 111 | 128 |

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# THE RELATION OF DONACIA LARVAE (CHRYSOMELIDAE: COLEOPTERA) TO DISSOLVED OXYGEN [1]

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The larvae of *Donacia* pass their life under water even though they do not possess any of the usual structural modifications for aquatic existence. They are equipped with a pair of caudal spines which at least in some instances may be used to penetrate the tissues of aquatic plants. The structure of the caudal spines and that of the respiratory system has been studied by several authors. Most previous investigators agree that the larvae use oxygen contained in air spaces of submerged parts of aquatic plants and that the caudal spines function in gaining access to this oxygen.

In this paper it is not denied that the larvae may use some oxygen from the air spaces of aquatic plants but circumstances lead to the belief that they secure oxygen in an additional way. From statements in the literature and from the writer's observations on submerged, laboratory-maintained larvae it is evident that they can live for a long time without penetrating the aquatic plants with their caudal spines. Early in this investigation it became apparent that the larvae either can use dissolved oxygen or can continue to live for a long time without oxygen. Since it has been suggested that the caudal spine might function like a gill in securing dissolved oxygen it was necessary to establish the importance of caudal spines for life in water without plants.

The larvae of most species in the region of Douglas Lake, Michigan, spend their complete larval life in the bottom mud or sand feeding on roots or rhizomes of aquatic plants. Some species spend either the whole or a part of their larval life, on portions of aquatic plants surrounded by water rather than by mud or sand. Since

larvae of the latter group often live where dissolved oxygen content of the water is high it seems apparent that if any *Donacia* larvae can use dissolved oxygen these should be able to do so. Larvae of three species were chosen as experimental animals. (1) *Donacia cincticornis* Newman larvae are always found in the mud with their caudal spines inserted into the root tissue of *Castalia odorata*. (2) *Donacia proxima* Kirby larvae occur in mud or sand with their caudal spines inserted into rhizomes of *Nymphaea advena* but most of the larvae, large and small, are found between the bases of leaf petioles. (3) *Donacia subtilis* Kunze larvae live on the roots of various aquatic plants but most of them are found between the leaves of *Sparganium* spp. Larvae of this species, used for experimentation, were collected from *Sparganium* plants growing in water where the oxygen content was higher than the water used in the experiments.

An investigation now in progress is being undertaken to determine whether all species of *Donacia* actually penetrate the tissues of aquatic plants with their caudal spines. Analyses of the water are also made to determine the amount of oxygen present in varied situations in which *Donacia* larvae live. Preliminary results indicate that *D. subtilis* and *D. proxima* can live on aquatic plants without penetrating the tissues with their caudal spines.

• This paper is the third in a series dealing with some Northern Michigan Donaciini. The first paper is concerned with the morphology of the immature stages (Hoffman, '40a) and the second with the limnological relationships of the group (Hoffman, '40b).

The writer wishes to express his indebtedness to Professor Paul S. Welch who directed this work and to various

other associates for valuable suggestions and aid.

## RESPIRATION

### *Historical*

The first important explanation as to how the larvae obtain their oxygen was presented by Perris ('48). He believed that there is no open spiracle at the base of the spine but in its place there is a thin membrane through which oxygen from the water passes by diffusion. Sanderson ('00) assumed the possibility of the caudal spine functioning as a tracheal gill. He claimed that the spiracle at the base of the spine is open and was inclined to believe that the caudal spines are so constructed that they can remove oxygen from the plant or water.

Other investigators agreed that the oxygen supply comes from the air spaces of the plant but differed as to the method by which it is obtained.

MacGillivray ('03) and Deibel ('11) agreed that the oxygen enters the tracheal system through the open spiracle at the base of the caudal spine and that the canals in the spines are not open to the tracheal system. Both authors were aware that the spines are inserted into the plant and believed that this act starts an outflowing of the air within the plant which finally reaches the open spiracle and thence into the tracheal system.

Schmidt-Schwedt ('89) and Böving ('10) believed that there is no hindering wall to the passage of gas from the canals of the caudal spine to the tracheal system. Böving believed that the canals of the caudal spines are closed by a thin membrane and Schmidt-Schwedt described openings to the outside. Both of these authors agreed that the air passes from the air spaces of the plant into the canals of the spine, Böving believing that the passage is by diffusion and Schmidt-Schwedt through the openings on the dorsal part of the spine. Schmidt-Schwedt and Böving, from studies on the spiracular split, concluded that the spiracle can be used for expiration only.

Most of the investigations on respiration of the larvae of *Donacia* have been of a morphological nature. Böving ('10), Deibel ('11) and Ege ('15) have done some experimental work and all have concluded that the larvae are unable to use dissolved oxygen. But, only one, Ege, actually made tests on the amount of oxygen present during the experiments. Unfortunately, he did not carry his experiments over a period of time long enough to be significant. Ege made some analyses on the amount of oxygen actually present in the roots and rhizomes of aquatic plants and, although he always found oxygen present, he concluded that it is low, which is in direct contradiction to the opinion of some of the other authors.

### *Experiments*

*Water Used in Experiments.*—The water used in the following experiments came from 2 sources and will be referred to as tap water and pump water.

Tap water is that supplied in the water system at the University of Michigan Biological Station. It is pumped from a well and then stored in a closed reservoir on a hill above the Station. The water used in the oxygen consumption experiments described below was taken directly from the laboratory taps into a carboy with the aid of a piece of rubber tubing. From time to time, this water was analyzed and found to be virtually constant in its chemical conditions. The following data indicate the principal chemical features. Free carbon dioxide, 3.0 p.p.m.; phenolphthalein alkalinity in p.p.m. as calcium carbonate, 0.0; methyl orange alkalinity in p.p.m. as calcium carbonate, 160; pH, 7.4; conductivity, 225 reciprocal megohms.

The water referred to as pump water was taken from a well made by driving a pipe deep into the sand. After operating the pump for a short time to insure that it was filled with new water lifted from the sand below, a long piece of rubber tubing was inserted through the top of

the pump and into its water-filled internal cavity, to the proximity of the uppermost valve. After a flow of the water through the rubber tube was established, pumping was begun and the other end of the tube inserted to the bottom of a carboy. The pumping was then continued until the carboy had been overflowed 3 times its capacity. By this method, water poor in oxygen could be secured. The following data indicate other chemical features which vary little. Free carbon dioxide, 7.0 p.p.m.; phenolphthalein alkalinity in p.p.m. as calcium carbonate, 0.0; methyl orange alkalinity in p.p.m. as calcium carbonate, 125; pH, 7.0; conductivity 225 reciprocal megohms.

*Submergence Tests.*—D e i b e l ('11) found that larvae lived in water for 4 weeks but attached more significance to his experiments showing that larvae survived for 17 days in water poor in oxygen. Deibel made no actual analyses of his *" sauerstoffarmen Wasser."* To determine how long submerged larvae can live, the writer immersed several in tap water having a known oxygen content. To be certain that the larvae would remain submerged, each was placed in a separate empty glass tube the 2 ends of which were covered with grit cloth. Each tube was then quickly submerged in an aquarium. Submergence forced the air out of the tubes causing the larvae to be entirely surrounded by water. At definite intervals the larvae were observed to determine if air bubbles had collected in the tube. Oxygen analyses of the aquarium water were made at this time. Larvae in the tubes were of two kinds, namely, normal larvae and larvae with the caudal spines removed. These spines were removed from some of the larvae to determine whether they are necessary for life in water. All normal larvae were alive and very active after 21 days of submergence in water in which the oxygen varied from 4.0 to 4.6 cc. per liter. The larvae with spines removed died after a submergence of 10 days. This experiment does not prove that the larvae

use dissolved oxygen. However, it does show that the larvae, both normal and experimental, are able to live in continuous submergence for a long time, remaining very active during the entire experiment. In contrast to Böving's findings, it was noted that larvae with caudal spines removed did not live as long as normal larvae, at least in water with an oxygen content of 4.0 cc. per liter.

*Oxygen Consumption Tests.*—In an experiment, Ege ('15) analyzed the water in which larvae had been submerged for an hour. The amount of oxygen used in his experiment was so small that he concluded that if the animal obtains any oxygen from the water it cannot be important as far as respiration is concerned.

In order to determine whether the larvae are able to use dissolved oxygen, tests were made on specimens representing several species. Larvae for these tests were submerged in 250 cc. glass-stoppered bottles which were placed in an aquarium. From time to time, the bottles were removed and the larvae extracted by means of a long forceps after which the controls and experimental bottles were analyzed for dissolved oxygen content. The analyses were made by the Rideal Stewart modification of the Winkler method as outlined in Standard Methods for the Examination of Water and Sewage, by the American Public Health Association ('36).

Tap water used in these experiments was collected through a hose directly into a carboy overflowed 3 times its capacity. Test bottles were then filled with water drawn from the bottom of this carboy and each 250 cc. bottle was overflowed 3 times its capacity. Three bottles were used for each experiment, 2 for controls, and 1 for the larvae. The water in the first control was analyzed at the time the experiment was started in order to determine if any oxygen was lost in the second control during the course of the experiment. In all experiments, the controls did not change outside the limits of the error of the method. In the third bottle, the

TABLE I.  *Table showing dissolved oxygen used by submerged larvae of three species of Donacia. Amount of dissolved oxygen present in control and experimental bottles, duration of experiment and condition of larvae also indicated.*
*Series A.  Donacia proxima.  Temperature— 20° C.  Two larvae used in each experiment.*
*Series B.  Donacia cincticornis.  Temperature —16° C.  Three larvae used in each experiment.*
*Series C.  Donacia subtilis.  Temperature— 16° C.  Five larvae used in each experiment.*

| O₂ (cc. per l.) | | | Time (hours) | Condition |
|---|---|---|---|---|
| Control | Experiment | O₂ consumed | | |

| | | A. Donacia proxima | | |
|---|---|---|---|---|
| 3.45 | 0.03 | 3.42 | 120 | Alive |
| 3.52 | 0.03 | 3.49 | 120 | 1 dead |
| 3.43 | 0.03 | 3.40 | 120 | Alive |
| 3.45 | 0.03 | 3.42 | 120 | Alive |
| 3.45 | 0.03 | 3.42 | 96 | Alive |
| 3.52 | 0.03 | 3.49 | 120 | Alive |
| 3.46 | 0.03 | 3.43 | 96 | Alive |
| 3.38 | 0.03 | 3.35 | 120 | Alive |
| 3.45 | 0.03 | 3.42 | 96 | Alive |
| 3.38 | 0.03 | 3.35 | 96 | Alive |
| 3.48 | 0.04 | 3.44 | 96 | Alive |
| 3.41 | 0.03 | 3.38 | 216 | 1 dead |
| 3.21 | 0.03 | 3.18 | 120 | Alive |
| 3.03 | 0.03 | 3.0 | 216 | 2 dead |

| | | B. Donacia cincticornis | | |
|---|---|---|---|---|
| 1.99 | 0.03 | 1.96 | 144 | Alive |
| 2.22 | 0.13 | 2.09 | 144 | Alive |
| 2.19 | 0.03 | 2.16 | 144 | Alive |
| 2.19 | 0.06 | 2.13 | 144 | Alive |
| 2.41 | 0.03 | 2.38 | 192 | Alive |
| 2.45 | 0.06 | 2.39 | 192 | Alive |
| 2.47 | 0.13 | 2.34 | 192 | Alive |
| 2.45 | 0.03 | 2.42 | 144 | Alive |
| 2.68 | 0.03 | 2.65 | 192 | 2 dead |
| 2.68 | 0.03 | 2.65 | 120 | Alive |

| | | C. Donacia subtilis | | |
|---|---|---|---|---|
| 3.2 | 2.4 | 0.8 | 22 | Alive |
| 3.15 | 0.15 | 3.0 | 48 | Alive |
| 3.1 | 0.1 | 3.0 | 48 | 1 dead |
| 3.1 | 0.07 | 3.03 | 62 | Alive |
| 3.15 | 0.15 | 3.0 | 48 | 1 dead |
| 3.15 | 0.07 | 3.08 | 48 | 1 dead |

larvae were introduced quickly to prevent them from carrying in an air bubble. The larvae, collected the day before the experiment, were carefully washed in several changes of water before being placed into the test bottles. These bottles were then submerged in an aquarium and

the temperatures were recorded twice daily by means of a maximum-minimum thermometer. The larvae, active at the beginning of the experiment, became very active and then inactive near the termination. Whenever the larvae became inactive they were removed after which the water in the control and in the test bottle was analyzed. After the removal of the larvae from the bottle, they were put into fresh water and watched for signs of life. If they were taken out at just the right time, even though they were quiet in the bottles, they would become active when put into fresh water.

The results of these experiments on 3 different species will be found in table I. In all species, the larvae used dissolved oxygen. In series A on *Donacia proxima*, the larvae reduced the oxygen to 0.03 cc. per liter. In some cases, the larvae would become very active and then quiet in 96 hours while in others they would not become inactive until 120 hours had elapsed. All analyses showed that when the larvae became inactive the oxygen content of the water had reached 0.03 cc. per liter. In 2 instances, however, the experiments were allowed to go beyond the critical stage without analyzing the water until the end of 216 hours. It was found that the oxygen was not removed beyond 0.03 cc. per liter even though the 2 larvae had died previously.

Series B, dealing with experiments on *Donacia cincticornis*, shows about the same results as those for *Donacia proxima* except that in the former species some of the larvae became quiet before the dissolved oxygen reached 0.03 cc. per liter.

Series C, concerned with *Donacia subtilis*, shows that the larvae did not reduce the oxygen content below 0.07 cc. per liter. Some of the larvae became inactive and even died before this oxygen content was reached.

From these experiments it is apparent that normal larvae were able to consume dissolved oxygen from the water. It was found that in the presence of sufficient oxygen the larvae were active and when

the oxygen content was lowered to the threshold the larvae became very active and then inactive. These experiments also show that the threshold of *Donacia subtilis* is higher than it is for the other species.

*Low Oxygen Resistance Tests.*—The next question is whether it is ever possible for larvae to live in water with a very low oxygen content. Böving's and Deibel's experiments both indicate that this is possible. Böving found that larvae can live submerged for 10 days in oil, in boiled water and in bog water. Deibel found that he could keep larvae alive for a period of 17 days in water poor in oxygen. It also seems evident that the larvae, at least at certain times in nature, may find themselves in a position where the oxygen content of the water is low.

The writer's investigations on oxygen consumption completed up to this time showed that the larvae, after lowering the oxygen content, were never able to live longer than 96 hours after the critical point had been reached. In order to settle this point, larvae were put in 250 cc. bottles and the same technique was pursued as in the preceding experiments except that in this series pump water with a low oxygen content was used. The oxygen content of this water at the beginning of the experiment was 0.26 cc. per liter. The larvae became inactive very soon after being introduced into these bottles but were revived upon removal at the end of 168 hours. The larvae did not show any increased activity before becoming inactive. The oxygen content at the time of removal was 0.03 cc. per liter. There were only 4 mortalities in 13 test bottles.

The experiment described above shows that the larvae are able to live in water low in oxygen, becoming inactive promptly but not dying as soon as those in the previous oxygen consumption experiments.

*Caudal Spine and Respiration.*—From the submergence tests of larvae with the spines removed one is led to believe that

TABLE II. *Table showing results of experiments performed to determine the importance of the caudal spines in the removal of dissolved oxygen from water. Amount of dissolved oxygen present in control and experimental bottles, duration of experiment and condition of larvae also indicated.*

*Series A. Larvae of Donacia proxima with spines removed. Temperature—21° to 26° C. One larva used in each experiment.*

*Series B. Larvae of Donacia proxima. Temperature—21° to 26° C. One larva used in each experiment. (a)—control bottle with glass stopper, (b)—control bottle with cellophane-paraffin cap, (c)—bottle with cellophane-paraffin cap and containing a free larva, (d)—bottle with cellophane-paraffin cap and containing a larva in a brass cage, (e)—bottle containing a larva with its caudal spines inserted into a cellophane-paraffin cap.*

| O₂ (cc. per l.) | | | Time (hours) | Condition |
|---|---|---|---|---|
| Control | Experiment | O₂ consumed | | |
| **SERIES A** | | | | |
| 2.1 | 1.75 | 0.35 | 28 | Alive |
| 2.0 | 0.65 | 1.35 | 28 | Alive |
| 2.0 | 1.1 | 0.9 | 28 | Alive |
| — | 0.03 | 1.97 | 28 | Dead |
| 2.15 | 0.06 | 2.09 | 46 | Alive |
| — | 0.5 | 1.65 | 46 | Dead |
| — | 0.03 | 2.12 | 46 | Alive |
| 2.0 | 0.03 | 1.97 | 52 | Dead |
| 2.15 | 0.06 | 2.09 | 52 | Dead |
| 2.0 | 0.06 | 1.94 | 52 | Alive |
| **SERIES B** | | | | |
| (a) 2.6 (b) 2.6 (c) 1.55 | 1.05 | 36 | Alive |
| — (d) 1.35 | 1.25 | 36 | Alive |
| — (e) 0.04 | 2.56 | 36 | Alive |
| (a) 2.6 (b) 2.6 (c) 0.95 | 1.65 | 48 | Alive |
| — (d) 1.1 | 1.5 | 48 | Alive |
| — (e) 0.6 | 2.0 | 48 | Alive |
| (a) 2.6 (b) 2.7 (c) 0.75 | 1.95 | 60 | Alive |
| — (d) 0.15 | 2.55 | 60 | Alive |
| — (e) 0.25 | 2.45 | 60 | Alive |
| (a) 2.6 (b) 2.3 (c) 0.03 | 2.27 | 72 | Alive |
| — (d) 0.03 | 2.27 | 72 | Alive |
| — (e) 0.03 | 2.27 | 72 | Alive |
| (a) 3.1 (b) 2.5 (c) 0.03 | 2.47 | 96 | Alive |
| — (d) 0.06 | 2.44 | 96 | Alive |
| — (e) 0.03 | 2.47 | 96 | Alive |

the spine might play a part in securing dissolved oxygen. Thus far, it has been found that normal larvae are able to use dissolved oxygen and that they can live for 168 hours in water in which the oxygen is low. It, therefore, seems possible that they might be able to live in water with their spines removed because of their

ability to live for a period in a dormant state without oxygen. But, the experimental larvae in the submergence tubes were not in a dormant state; on the contrary they were much more active than the larvae in the low oxygen resistance tests. In order to determine the importance of the spines in the securing of dissolved oxygen, the spines were removed from a number of larvae and consumption experiments tried on them according to the technique outlined in the previous experiments. Table II, series A, concerning *Donacia proxima*, summarizes the results of these experiments, showing that larvae are able to use oxygen with their spines removed. Their actions, nevertheless, were quite different from normal larvae in that if they were not removed as soon as they became quiet they could not be revived. Gas bubbles appeared at the cut portion of the spine but remained there only momentarily.

These experiments seem to indicate that the spine is not the organ of respiration in removing oxygen from the water and that the peculiar behavior of the de-spined larvae might be caused by gas leakage of the caudal spines. The combination of low oxygen tension and the spine removal brings about an earlier death than it does in the submergence tubes where the oxygen content was high.

The larvae without spines behaved in such an irregular manner when compared to normal larvae that a new technique had to be devised to remove the spines from the water. The first attempt was to put the caudal spines through a small hole in a piece of rubber dam; the larva was held in place by painting shellac over the distal ends of its spines. The dam was placed over a 250 cc. bottle which was filled to the top with water; by careful placement air bubbles were avoided. The larva was then completely submerged in the neck of the bottle with its caudal spines projecting up through the dam into a mass of shellac. The rubber dam was held in place over the neck of

the bottle by a rubber band, care being taken to avoid any wrinkles in the rubber dam. This cap was then covered with shellac so that the whole bottle was completely sealed. The larvae showed no deleterious effects either from handling or from the application of the shellac to the spines.

This experiment indicated that the larvae were still using oxygen. The experimental bottles showed that the oxygen content was reduced from 2.9 to 0.0 cc. per liter in 96 hours. However, the controls also showed that oxygen was being reduced although not as rapidly as in the experimental bottles. The more rapid reduction of oxygen in the experimental bottles signified some oxygen consumption but, due to the loss of oxygen by the controls, these experiments could not be used to furnish conclusive data. Tests made by placing the rubber and shellac directly into closed bottles showed that in 96 hours these substances removed every trace of oxygen from a bottle that originally contained 3.0 cc. per liter of oxygen.

Since rubber and shellac could not be used in experiments it was necessary to find other materials in which the oxidation rate is much slower. Each of several selected substances was placed in water in a 250 cc. bottle and the water analyzed after 96 hours. As a result of these tests two substances were chosen because of their very slow oxidation rate, namely, cellophane and paraffin. At the same time, other substances were tried which might play an important part in the preceding oxygen consumption experiments. Water containing larvae, recently dead, was analyzed and it was found that the amount of oxygen used by their bodies in 96 hours could hardly account for the oxygen decrease during the experiments in oxygen consumption. Water with detritus or excrement, carried into a dish with 30 larvae, was analyzed and showed little oxygen consumption. This analysis was made to be certain that bacteria which might be carried in with the larvae were

not responsible for the oxygen reduction.

Experiments were then performed to compare oxygen consumption of free larvae in a bottle and larvae attached to a cellophane-paraffin cap. This cap was composed of a sheet of cellophane stretched across the neck of a bottle, held in place by a rubber band, and completely sealed over with paraffin. In the preparation of some of the cellophane-paraffin caps the caudal spines of a larva were inserted through a small hole in a sheet of cellophane and held in place by paraffin. It was then placed over the neck of a bottle, held in place by a rubber band, sealed over and attached to the neck of the bottle by means of paraffin. Care was taken to avoid air bubbles in the neck of the bottle so that the larva was completely submerged but with its caudal spines out in the paraffin. A larva was also placed in a brass cage in the neck of one bottle to determine whether the position in the neck of the bottle is a hindrance to oxygen consumption. Table II, series B, shows the results of this experiment on the larvae of *Donacia proxima*. Five bottles were prepared for each experiment: *a* was a control bottle with a glass stopper, *b* was a control bottle with a cellophane-paraffin cap, *c* was a bottle with a cellophane-paraffin cap and contained a larva resting on the bottom, *d* was a bottle with a cellophane-paraffin cap and contained a larva in a brass cage, *e* was a bottle containing a larva whose caudal spines had been inserted into a cellophane-paraffin cap. The experiments show that the larvae can use dissolved oxygen as efficiently without the spines as with them. In fact, at the beginning of the series of experiments they used it faster than the larvae in the cage and those at the bottom of the bottle. This may have been due to greater activity of the larvae in their unusual situation. In other respects larvae with their spines in the cellophane-paraffin cap behaved in a normal fashion.

These experiments show that the larvae with their spines out of water are just as capable of using dissolved oxygen as those in the bottom of the bottle. Since there is no special structural adaptation for utilizing dissolved oxygen it seems necessary to conclude that such respiration is cutaneous.

Böving ('10) suggests that the caudal spine may serve as an "organ of fixation" as well as a device for securing oxygen from the air spaces of the plant. The larvae of *D. subtilis* and *D. proxima* can apparently live on aquatic plants without inserting their caudal spines. The larvae of these two species may rely upon the pressure of the opposing leaves or leaf petioles to maintain their positions on the plant. They insert their caudal spines into the plant tissue while constructing their cocoons. Larvae of *D. cincticornis* are usually found with their caudal spines penetrating the root tissue of *Castalia odorata*. At the present time it has not been ascertained whether the larvae of the above species insert their spines for purposes of respiration or to maintain their positions.

## SUMMARY

1. Most of the previous investigators contend that oxygen used by larvae of *Donacia* comes entirely from the air spaces in aquatic plants and that the larvae gain access to this oxygen by penetrating the tissue of the plant with their caudal spines.

2. Larvae of *Donacia* were kept alive and active in continuous submergence in water without plants for 21 days. The oxygen in the water varied from 4.0 to 4.6 cc. per liter.

3. *Donacia* larvae lived in a dormant state for 168 hours in water in which the oxygen was low at the beginning of the experiment.

4. *Donacia* larvae on which tests were performed used dissolved oxygen. Most of the larvae of *D. proxima* and *D. cincticornis* consumed all but 0.03 cc. per liter, while in *D. subtilis* the threshold was always somewhat higher.

5. The caudal spines are not important for the utilization of dissolved oxygen in respiration. Since there is no other structural modification, it seems necessary to conclude that dissolved oxygen is secured cutaneously.

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# A DISCUSSION OF THE APPLICATION OF A CLIMATO-LOGICAL DIAGRAM, THE HYTHERGRAPH, TO THE DISTRIBUTION OF NATURAL VEGETATION TYPES

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## INTRODUCTION

Perhaps no problem is of greater interest to the ecologist than that of correlating natural vegetation with climatic factors. In spite of this extreme interest, no great success has attended the many efforts in this direction. This may be due both to complications which arise from the effect of edaphic conditions in nullifying those of climate, and also because climatic data as at present recorded may not represent the most important factors which control the distribution of vegetation.

Because of their obvious and limiting influence in this relationship, the factors of temperature and rainfall have received the most attention. One of the first vegetational-climatic classifications was that of Mayr (Baker '34) in which the vegetation was delimited according to temperature. Though the divisions made by him show a general conformity, they are only broadly applicable. Koppen (James '22) later developed a scheme in which the moisture relationship received greater attention. Because each of these schemes was based on but one of these two important climatic factors, they fail in those areas where the factor used is not the limiting one.

Perhaps the most common of the schemes for classification in America is that devised by Merriam (1898). In this the summation of temperatures during the growing season was used to define the limits of life zones. Because of the obvious effect of the moisture factor, the United States, to which it applies, was divided into a moist eastern and an arid western division. Though this scheme is not soundly based (Livingston and Shreve '21), the divisions correspond rather closely with natural vegetation units. For this reason the nomenclature is widely used even though the basis of it is not held in high repute. The work of Livingston and Shreve ('21) was undertaken in a somewhat different manner from other studies in this direction. The United States was first divided into provinces which seemed to be units of vegetation and then the climatic factors responsible for this division were sought. The writers conclude that a better interpretation of climatic factors together with a more thorough understanding of the effect that these have on the physiological processes are needed before there can be any adequate correlations.

## METHODS

The present study is based upon graphical presentation of temperature and precipitation, recorded as monthly means, both being recorded on the same diagram. While it is recognized that extremes rather than means may be more important in distribution of vegetation, particularly with reference to individual species, broad divisions of vegetation should show a relationship to mean conditions.

The nomenclature of the diagrams used was first standardized by Taylor ('20a). Two types were employed by him. The first using monthly temperatures and rainfall were called hythergraphs. Where humidity was used in place of precipitation as the ordinate, the figures were referred to as climographs. These had previously been used by Ball ('10) in Egypt to determine the suitability of certain oasis areas for human habitation. Taylor ('20b) adopted them in determining the suitability of various parts of the Australian continent for human habita-

tion and attempted to predict the development of these areas on the basis of his findings. A very detailed study was made by Johnson ('24) of the conditions obtaining in the densely populated sections of the world in respect to sheep production. A general diagram was made based upon a number of individual stations, which he assumed marked the climatic limits for successful sheep production. From the generalized diagram thus obtained he attempted to explain the factors limiting sheep production in other sections and the reason for poor sheep years.

This type of diagram has also been used in the study of other animals to explain the success or failure of these animals in certain areas. Thus, Davidson (original not reviewed, reported by Shelford '29) concluded that the success of Hereford cattle on western ranges is due to their having been developed in a more arid climate than was the shorthorn. He failed, however, to get a close correlation as did Johnson. Steggerda ('29) explains the success of chicken breeders in Petaluma, California, on the basis of the similarity of the climate there and the ancestral home of the chicken in India. Insects as well have been studied by this means and Sweetman ('29) concludes that irrigation sufficiently modifies the humidity conditions in otherwise dry areas to permit existence of the Mexican bean beetle. Carter ('30) has used them to predict the probable spread of the beet leafhopper. Twomey ('36) applied them in a study which attempted to forecast the distribution of some introduced birds.

Most of the instances in which these diagrams have been employed have been in the ecology of animals. Though they have been employed to picture conditions in vegetation types (Allee '26) no known efforts have been made to correlate the distribution of vegetation with the diagrams.

The diagrams are constructed by plotting the mean monthly temperatures for the selected weather station over the pre-

cipitation for the same month. This is done for the twelve months of the year, these points then being connected by lines. The result is a closed figure showing the progression of temperature and precipitation throughout the year.

The composite diagrams are formed by superimposing all the diagrams for any one vegetation type upon each other and bounding the outermost points of them all. These composite diagrams do not necessarily exhibit any points to correspond to the months of the year.

Data were collected for eight vegetation types: the southern desert shrub, the sage brush, the boreal forest, the deciduous forest, the short and tall grass areas of North America, the Russian Steppe, and the Pampas region of the Argentine. The composite diagrams of all but the two grass areas of North America are shown in figures 1 to 3 respectively. The two exceptions were considered in greater detail than the other areas, data from these areas being shown by states.

DISCUSSION

Examination of the figures reveals the fact that each vegetation type selected has a distinct hythergraph pattern. The boreal forest is characterized (fig. 1) by a wide range of temperatures, with fairly high summer and low winter records. Precipitation is not high for any one month, summer precipitation being only slightly higher than in the other seasons of the year. In most of the stations this high rainfall was for a very short period of only one or two months.

The deciduous forest (fig. 1) is shown to have a fairly even winter-summer rainfall, the highest monthly catches being recorded in the late winter and spring, and again in the summer. The mean monthly temperature range does not exceed 60 degrees in most instances.

The sagebrush diagrams (fig. 2) differ somewhat from those previously described, in that the winter months mark the period of greatest rainfall, though a

few stations show a secondary maximum during one of the summer months. Of the stations for which data were collected,
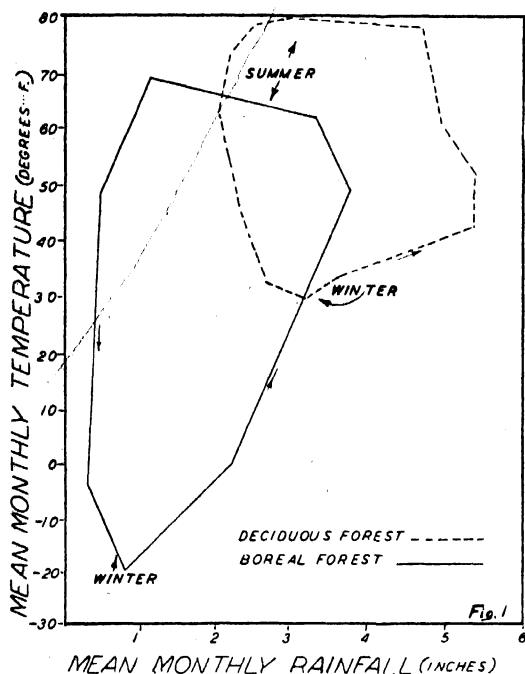


FIG. 1. Composite hythergraphs of boreal forest and deciduous forests of North America.
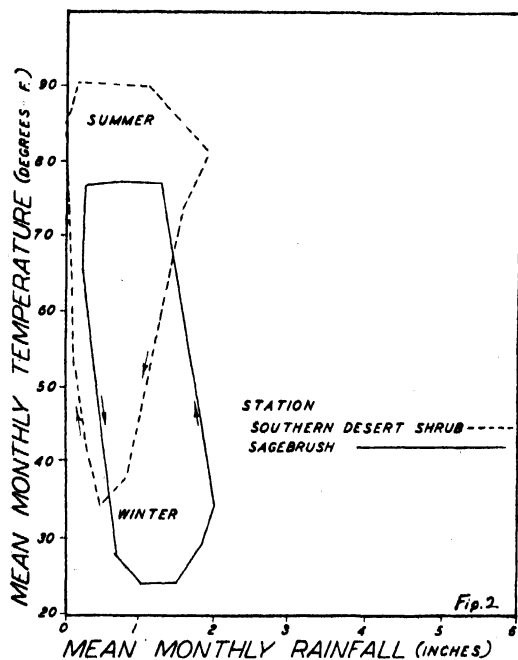
none had a mean rainfall which for any month exceeded 2 in., while the lowest monthly records in the summer were as low as 0.2 in.

The graph of the southern desert scrub (fig. 2) is in general outline similar to the sagebrush areas. It is, however, entirely different in that instead of proceeding counter-clockwise around the figure in following the consecutive months the direction is clockwise. That is, the rainfall becomes less from midwinter to almost no precipitation during the spring and early summer, rises to the maximum for the year in late summer or early fall, then progressively falls off to the minimum. This is the only area of those studied that follows this succession.

The grassland areas were investigated somewhat more thoroughly than the other vegetation types. Because of the broad area available and the opportunity for securing data, the North American grasslands seemed to offer the best area for study. Records were secured also from two other grassland regions in order to discover the agreement between grassland



FIG. 2. Composite hythergraphs of southern desert shrub and sagebrush areas in North America.
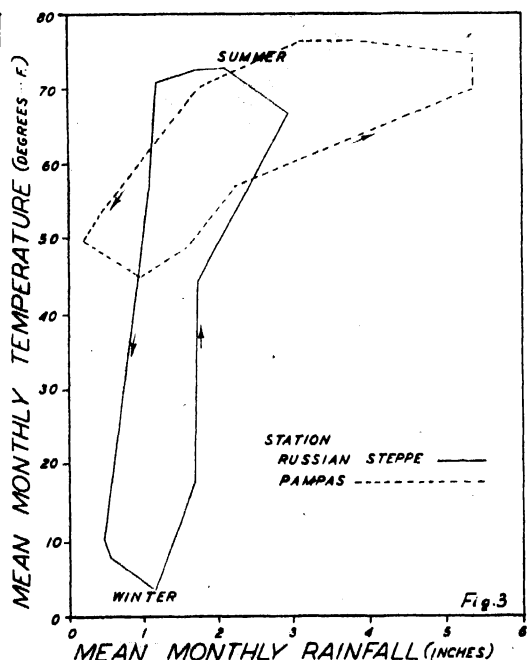


FIG. 3. Composite hythergraphs of Russian steppe and Pampas region of the Argentine compared.

areas in different regions of the world. Those taken from the Russian steppes are of particular interest (fig. 3). Though some of them show a rather close resemblance to grasslands of North America, the excess of rainfall in the summer period over that of the winter is not so great. This would indicate that the area is more nearly desert or semi-desert than American grassland. However, the difficulty of making any conclusions in this region is apparent when it is known that the area classed as steppe is made up of different kinds of vegetation varying from that of meadow to a semi-desert type of grass (Keller '37).

Figure 3 shows the hythergraph of the Pampas area in South America. Here again is noted the great percentage of the rainfall coming in the summer period as compared with the winter. However, the temperature range is rather low and as is shown by comparison to figure 8 has some characteristics in common with the tall grass area in its southern extremities, Texas and Oklahoma.

Figures 4 to 10 show the diagrams of the tall and short grass areas by states. Whenever both types of vegetation occur, diagrams for both areas are shown together. Where only one grass type occurs within a state the tall and short grass diagrams of states of about the same latitude are shown on the same figure. Throughout it is noted that the amount of moisture received during the summer period is considerably greater in the case of the tall grass areas. There is, however, one interesting exception to this. In North Dakota (fig. 4) the maximum mean monthly rainfall in the short grass areas is essentially equal to that of the tall grass area of the same state. It is of interest to note, though, that this occurs only during one month, while in the months preceding and following this period, rainfall is slightly higher in the tall grass area. This more extended period of high rainfall and the generally lower temperatures during the summer months might account for the difference of the vegetation of the two areas.

As further evidence of the value and shortcomings of the diagrams in pointing
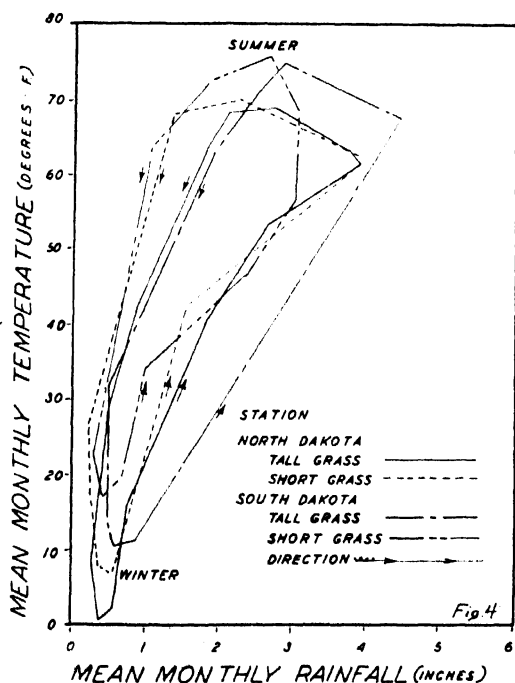


FIG. 4. Composite hythergraphs of the tall and short grass areas of the Dakotas.
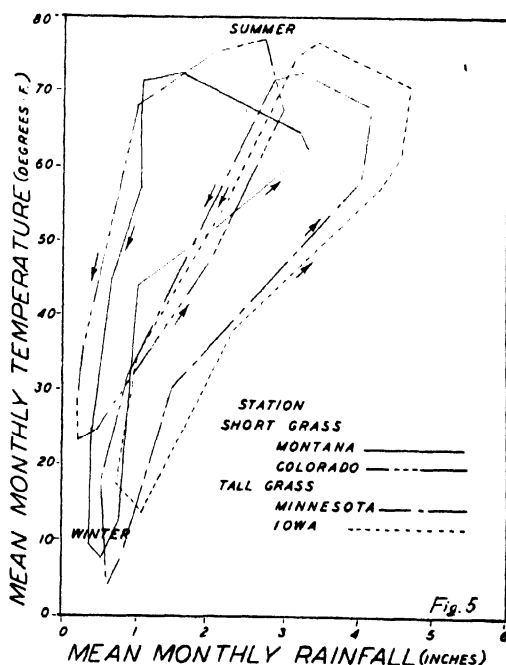
FIG. 5. Composite hythergraphs of tall and short grass areas.
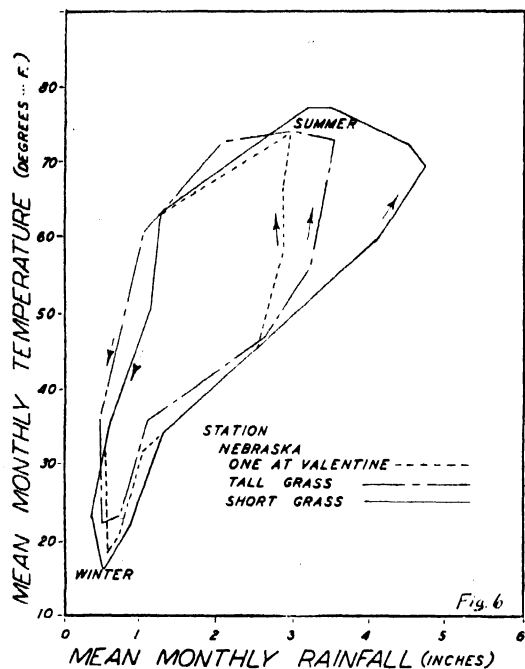
FIG. 6. Composite hythergraphs of tall and short grass areas in Nebraska with one individual station (Valentine) in the tall grass area.

FIG. 7. Composite hythergraphs of Kansas tall and short grass areas.



FIG. 8. Short grass area of Texas panhandle and Oklahoma compared to hythergraphs of the grass areas of the same state.

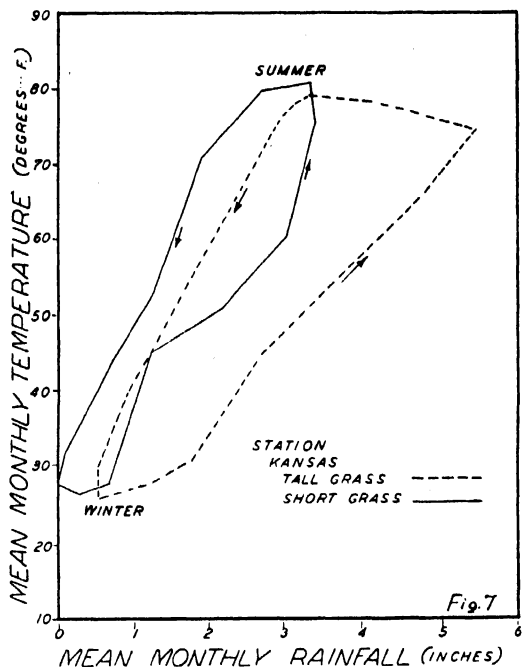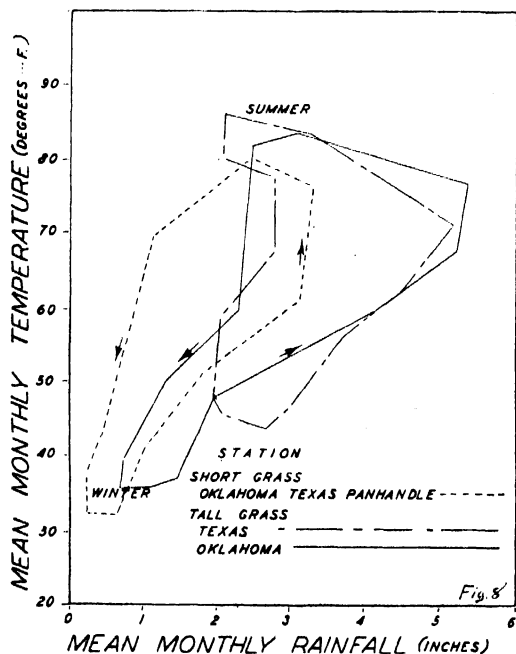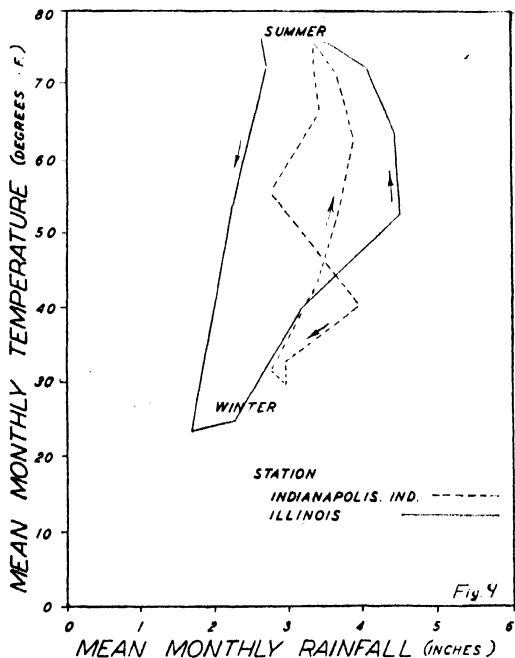FIG. 9. Composite hythergraph of the Illinois grasslands compared to a station within the deciduous forest.
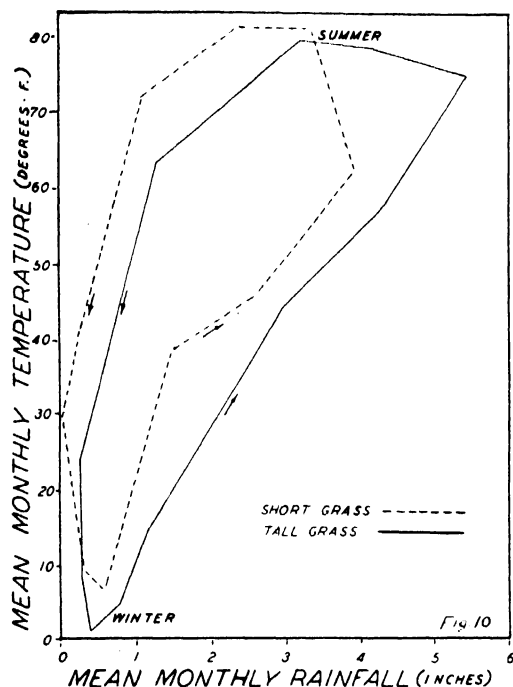
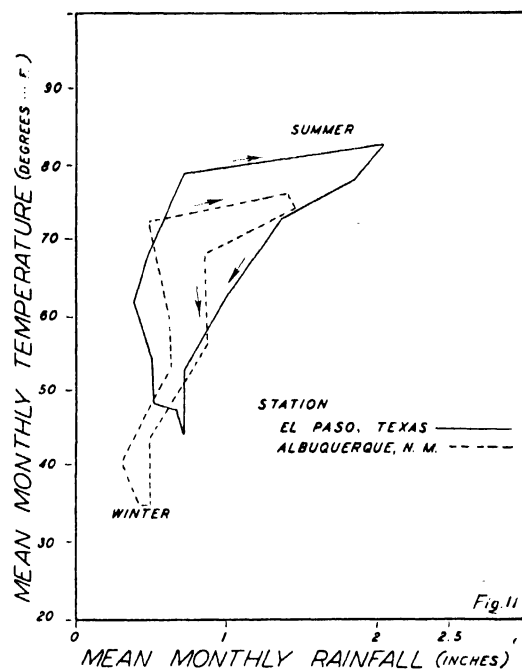FIG. 10. Composite hythergraphs of North American tall and short grass areas.



FIG. 11. Hythergraph of El Paso, Texas, located in semi-desert grass, compared to Albuquerque, New Mexico, shown by Shantz and Zon to be in the short grass type.

to the character of vegetation present on an area, the case of Valentine, Nebraska, is cited (fig. 6). Although included in the tall grass vegetation type, the diagram most closely follows the short grass hythergraph of the same state which would indicate that the climate would not support a tall grass vegetation. This apparent contradiction is explained by the fact that this station is in the sandhill section where favorable edaphic conditions permit the tall grass to grow. It also points to a weakness in the use of the figures since such conditions may alter the vegetation in any one locality.

The case of the Illinois prairie is also of interest (fig. 9). Though shown on maps of vegetation as being an area of tall grass, the hythergraphs of stations in the area depart somewhat from the typical grassland figure and approach diagrams of the deciduous forest (fig. 9). This would seem to confirm the conclusions of writers (Shantz and Zon '24 and Sampson, H. C. '21), that the area is not grass-

land climax, but a true forest climax held in a grassland stage by other influences.

Of especial interest is the case of Albuquerque, New Mexico (fig. 11). This area is shown on the vegetation type map of Shantz and Zon to be within the short grass area. Comparison of the hythergraph with that of El Paso, Texas, which is in the semi-desert grasslands shows a marked similarity between the two. In both cases the progression is clockwise, rather than counter-clockwise, as is true of most other diagrams. This would justify the work of Livingston and Shreve ('21) in placing this area in the semidesert grassland rather than in the short grass area.

It must be admitted that mean data as are here used may not be sufficiently critical to delimit the zones of vegetation except in a broadly general way. Ecologists have frequently pointed out that extreme rather than mean conditions may be most important in determining the areas occupied by species and floras

(Mason '37 and Good '31). This view is given support by the evident changes in the composition of vegetation during the drought of 1934 (Weaver and Albertson '36 and Ellison and Woolfolk '37). These studies suggest the possibility of using data of extremes rather than means, which do not indicate the stresses to which plants may at times be subjected, in correlating the distribution of vegetation with climatic records.

Although it is realized that the present study is not exhaustive, it is believed that enough evidence has been given to indicate the possibilities of such figures. It was impossible to examine the areas studied and hence the approach to or departure from optimum vegetation could not be noted, which makes the figures less critical than they might otherwise be. A further complicating circumstance is that weather bureau stations are not located with the idea of interpreting the habitat of vegetation and may not give the true index to the conditions to which vegetation is subject even though apparently located in a given vegetation type. Were these complications removed, these diagrams are believed to be of sufficient accuracy to reveal the limits of vegetation types.

## SUMMARY

Though the hythergraph frequently has been used to interpret climatic conditions, and particularly in reference to suitable environmental conditions for animals, it has not been used as an index in the determination of natural vegetation types.

Weather data were collected for eight vegetation types, the southern desert shrub, the sagebrush, the boreal forest, the short and tall grass areas of North America, the Russian steppe, and the Pampas region of Argentina.

The resulting figures reveal that there is a definite pattern exhibited for each vegetation type studied. This is expressed in the shape of the figure or the

clockwise or counter-clockwise direction exhibited by following the successive months of the year.

Using this normal hythergraph pattern as an index the data indicate that the Illinois prairie area is in the deciduous forest climax rather than true prairie. Likewise, the region in the vicinity of Albuquerque, New Mexico, would seem to be properly regarded as semi-desert grassland rather than short grass, a classification that is made by some phytogeographers.

Were climatic data to be secured from stations located with a view to interpreting as nearly as possible the conditions to which vegetation is subject, it is believed that the diagrams shown would delimit broad natural vegetation units.

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# BIOLOGICAL OBSERVATIONS IN MOUNTAIN LAKE, VIRGINIA [1]

R. E. COKER,[2] AND WAYLAND J. HAYES, JR.[3]

*Nature and Location.*—Mountain Lake in Giles County, Virginia, said to be the only natural lake of substantial size in the unglaciated part of the Appalachians, has been the subject of limnological record by Hutchinson and Pickford ('32). Situated at an altitude of 1200 m. (3970 ft.), it has a length of about 1.2 km. and a width of .4 km., with surface area of about 100 acres. The maximum depth has been given by Williams (*unpublished thesis,* University of Virginia) as 110 ft. but it is very difficult to get soundings of much more than 70 ft. Apparently there are, among great boulders on the bottom, pockets or crevices in which deeper soundings can be made.

During the summer of 1937, the class in Hydrobiology at the Mountain Lake Biological Station of the University of Virginia conducted studies on the Lake and certain of their observations are worthy of record. The common animal plankters found were the same as those recorded by Hutchinson and Pickford, viz., one calanoid copepod, *Diaptomus leptopus* Forbes; two cladocerans, *Diaphanosoma brachyurum* (Liévin) and *Daphnia pulex* (de Geer); two rotifers, *Conochilus unicornis* Rousselet and *Notholca longispina* (Kellicott); and the protozoan, *Volvox.* Dr. I. F. Lewis, Director of the Station, mentions that *Dinobryon* has been known to appear in such vast numbers (as is characteristic of this flagellate protozoan) as to discolor the water. In our net collections, made on many occasions from July 3 to July 21, it was never observed [4]—nor any protozoan other than *Volvox* and *Difflugia,* the former being conspicuous in virtually all collections, the latter rare in the plankton. Like the authors previously cited, we found a few species of desmids prominent in the plankton. Other algae will be mentioned later.

There is comparatively little shallow water except near the south end and rooted aquatic plants are not conspicuously abundant. Chief among such are the following: the water weed, *Elodea,* abundant near the southern end, but sparse at the other and deeper end; the quillwort, *Isoetes,* in tufts 6 to 12 inches high; the water plantain, *Alismo plantago-aquatica;* an unidentified grass, all generally distributed wherever there is shallow water; and the blunt spike rush, *Eleacharis obtusa,* very tall and common near the south end (plant identifications by Dr. Lewis).

*Transparency.*—The lake is surrounded by densely forested hills and we never noted any considerable degree of turbidity. Transparency by the Secchi disk was approximately 5.49 m. (18 ft.).

*Temperature Stratification.*—The thermocline was between 4.5 and 9 m. (15 and 35 ft.). In the epilimnion the temperature varied, with weather conditions and with depth, between 20° and 25.8° C. In the hypolimnion it ranged from 11° C. at about 9 m. to 8° C. at 22 m. (72 ft.). We found no change in temperature in the lowest 5 meters; Hutchinson and Pickford's record of 5.5° at 22 m. may have been taken over some spring in the bottom, or else the bottom conditions were quite different in 1931. The solid line in the graph (fig. 1) is from observations made July 16 by Jeanne Matthews, with readings for every foot from surface to 35 ft. and for every 2 or 3 ft. from 35 to 65 ft. Serial records made on several other days showed no

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[4] Later a single colony of *Dinobryon* was found in collections by Grover.
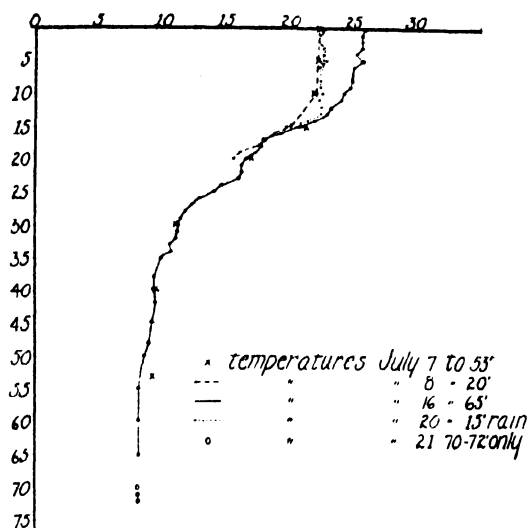
Fig. 1. Temperature, Mountain Lake at various depths (vertical) and on several dates (horizontal), July 1937.

notable differences in temperature below the epilimnion (fig. 1).

*Vertical Distribution of Plankton.*—To determine vertical distribution and diurnal migrations of Entomostraca in the epilimnion, series of collections at surface, 2 ft., 5 ft., 10 ft. and 20 ft. were made by Maude Hatcher and Alice Grizzard at intervals of 6 hours during a 24-hour period. A closing net with opening 95 mm. (3¾ inches) in diameter was hauled a distance of about 50 yds. over a course determined by cross bearings at each end. The depth of the lake along the line of observation was about 35 ft. at one end of the course and 65 ft. at the other, being about 75 ft. near the middle. The collections, after settling and reduction to a common volume of 10 cc., were subjected to counts with the use of the Rafter cell and micrometer eye-piece.

In the four collections at 11 P.M., 5 A.M., 11 A.M. and 5 P.M. (cir.), July 10 and 11, 1937, *Diaptomus* was regularly most abundant at 2 ft. At night the number dropped off notably from 5 to 20 ft. In the day collections (11 A.M. and 5 P.M.), when the peak at 2 ft. was most pronounced, the number of individuals was reduced at 10 ft. but there was indi-

cation of a second peak at or below 20 ft. Most notable was the crowding to the surface at night. This copepod is so brilliantly red that it can easily be seen by the naked eye in the clear water. One can lie on the dock in the daytime and see great numbers of swimming copepods, which are made even more conspicuous if looked at against a white background such as is afforded by the Secchi disk. Their brightness of color and relative opacity make them seem far more abundant than *Daphnia* and *Diaphanosoma* whose translucent bodies can only occasionally be distinguished. Near midnight the view of copepods seen by the use of a flashlight held above the water was most impressive, as they swarmed close to the surface. The nocturnal gathering just beneath the surface was well attested by the counts of the night collections; but, notwithstanding the great numbers found in the surface collections (3359 at 11 P.M., as contrasted with 207 at 11 A.M.), the number found at a depth of 2 ft. (4643) was still greater and approximately the same as in the day collection (4556).

*Diaphanosoma* crowded toward the surface at night, but with greater numbers at 2 ft. Comparatively few were found in the 10 and 20 ft. collections, the concentration being evidently in the upper 5 ft.; by 5 A.M., however, the greater number were below 5 ft. with the peak at 10 ft. At 11 A.M. the greatest number appeared at 20 ft. although the peak of abundance may have been below that level —the lowest at which observations were made in this series. At 5 P.M. the greatest numbers were at about 5 ft.

*Daphnia* also rose toward the surface at night, but not to the same degree as the copepods. The 2 ft. collection at night was more than five times as great as the surface collection. An early morning peak appeared at 5 ft. but by 11 A.M. the greater number of *Daphnia* were in the lower epilimnion or in the thermocline with greater concentration at or below 20 ft. At 5 P.M. a considerable number were

at the surface with again a peak at 5´ ft. and only a small number at 2 ft.

Considering the entomostracan collections as a whole, *combining species* and *hours,* there was, on July 10 and 11, little difference in total numbers at the surface and at 10 ft. and 20 ft. The 2 ft. level, or somewhere between 5 ft. and the surface, was the level of densest population. Considering the species severally for all hours, *Diaptomus* was most superficial in distribution and most abundant; it constituted 40 to 50 per cent of the catches of Entomostraca at every level, but more than half of them were taken at 2 and 5 ft. *Daphnia,* least superficial of the three, constituted a relatively greater proportion of catches in the deeper levels but the greater proportion of them (about one-half) were taken at 2 and 5 ft.

These observations of a single diurnal series are of interest in connection with a more extended study made by another student, and reported separately (Grover and Coker, '40). At that time (August) concentration of Entomostraca was at a somewhat lower level.

## THE NANNOPLANKTON [5]

*Procedure.*—Water used in making this study was obtained July 16, 1937, from different levels of the lake by the use of a Foerst water bottle. At the time of collecting the sky was overcast by clouds.

In preparation for the counts mentioned below, four tubes of water, each containing 16 cc., were centrifuged for 8 minutes at a speed of from 2700 to 3300 revolutions per minute. The top water in the tubes was then drawn off. The contents in the bottom of three tubes was stirred up and transferred to the fourth tube which was then recentrifuged for 3 or 4 minutes. This time was found sufficient to bring the organisms to the bottom. The centrifuging being completed, water was drawn off from the tube until one cubic centimeter remained. The organisms in the one cubic centimeter were

counted by the use of a Sedgewick-Rafter counting cell. Examples of the different kinds of organisms were measured by the use of an ocular micrometer. A magnification of approximately 215 power was used in the measurement.

*Results.*—The following kinds of nannoplankton were found:

1. By far the most numerous of all organisms examined was a colonial alga of the genus *Dictyosphaeriopsis* (identification checked by Dr. I. F. Lewis). The alga occurs in gelatin-like masses ranging in size from $16.2 \times 29 \mu$ to $66.5 \times 106.5 \mu$, the average diameter being in the order of 30 to 40 $\mu$. The cells of the algae measured $2.7 \times 2 \mu$.

2. Two species of the genus *Crucigenia* were found. One was *C. quadrata* Morren whose colony measured $2.7 \times 2 \mu$; the cells $5.4 \mu$ in diameter.

3. The other, *Crucigenia rectangularis* (Nägeli) Gay, had a colony measuring $13.5 \times 13.5 \mu$, the cells being $5.4 \mu$ in diameter.

4. A colonial alga, tentatively identified by Dr. J. M. Fogg as *Dimorphococcus lunatus* A. Braun, was found. The colonies examined ranged from $40.0 \times 43.2 \mu$ to $45.9 \times 49.4 \mu$, the cells from $2.7 \mu$ to $5.4 \mu$ in diameter, even within one colony.

5. A single specimen belonging to the genus *Anaebaena* was found. The cells, $5.4 \mu$ in diameter, occur in chain form. The colony found consisted of 24 units and measured $121.5 \mu$ in length.

6. Several specimens of an unidentified species of *Urococcus* were found. They measured approximately 24 $\mu$ in diameter including the gelatinous matrix.

7. A desmid, *Staurastrum curvatum* W. West, ranging in size from $18.0 \times 18.9 \mu$ to $21.6 \times 21.6 \mu$ was found.

8. One specimen of the diatom, *Tabellaria fenestrata* (Lyngb.) Kütz, was encountered. One other species was found but not identified.

9. Bacteria were numerous, especially at the bottom. No attempt was made to count them, since, with the magnification

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[5] Observations by Wayland J. Hayes, Jr.

used, a count of organisms so small as bacteria would not be significant.

10. Small, unidentified ciliates, 5 to 10 $\mu$ in length, were found in small numbers. (It is interesting to note that no flagellates were found although they might have been expected.)

Counts were made of the most numerous alga, *Dictyosphacriopsis*, as taken at various depths. The results are shown in the following table. The figures represent the number of colonies per cubic centimeter of lake water.

| | |
|---|---|
| Surface | 32.7 |
| 2 ft. | 264.6 |
| 5 ft. | 470.4 |
| 10 ft. | 723.8 |
| 20 ft. | 120.7 |
| 30 ft. | 62.2 |
| 40 ft. | 43.8 |
| 50 ft. | 15.4 |
| 60 ft. | 0 |

In the two samples counted to determine the relative abundance of the different forms, it was found that they occurred in proportions such that, for every 100 colonies of *Dictyosphacriopsis*, there were

0.14 Protozoa, 0.56 colonies of *Crucigenia*, 0.71 colonies of *Dimorphococcus lunatus*, 0.76 *Staurastrum curvatum* and 0.21 of various diatoms.

The graph (fig. 2) shows: (1) the vertical distribution of the nannoplankton, chiefly *Dictyosphacriopsis*, indicated by the solid line; (2) the distribution of Entomostraca, indicated by the broken line; and (3) the records of temperature, indicated by the dotted line. The depth scale for the lake, recorded on the ordinate, is the same for the three graphs. On the abscissa the quantity of algae is expressed (upper figures) in numbers of colonies per cubic centimeter of lake water. Since the amount of water passing through the Müller net was not measured, the figures employed in making the graph for Entomostraca do not represent absolute abundances, but only percentages of the highest number taken at any depth (10 ft. = 3.05 m.), taken arbitrarily as 100. The figures employed in computing percentages were furnished by William Grover and represent means of catches
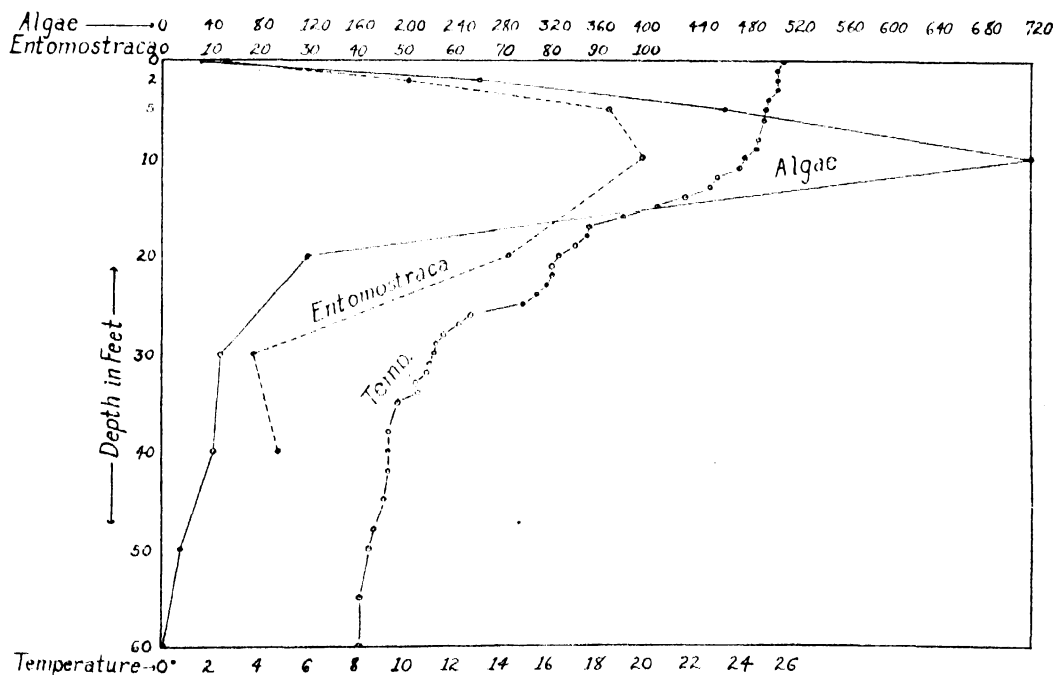


FIG. 2. Distribution by depth for algae of nannoplankton, Entomostraca and temperature, Mountain Lake. Observations on algae and temperature, July 16, 1937; Entomostraca—broken line, representing means of distribution by day, July 21–August 1, 1937.

taken at the several depths at about 2 P.M. for several days between July 13 and August 1. The temperature is indicated along the ordinate at the bottom.

*Conclusions.*—The graph (fig. 2) shows clearly that, at the time of observation, the algae were concentrated in the epilimnion (below the very top) and in the uppermost part of the thermocline (2 to 20 ft.) where doubtless both light conditions and temperature were favorable. [Visibility with Secchi disk 30 cm. in diameter 18 ft. (5.49 m.).]

*Straining Mechanism of Entomostraca in Mountain Lake.*—It is noteworthy that the crustacean plankton comprises exclusively species that feed by filtering or straining, there being no limnetic *Cyclops* to prey upon rotifers and other Crustacea. Several species of *Cyclops* of littoral habit are found in the lake. When a net was dragged over the *Chara* on the bottom at 18 to 20 ft., or deeper, there were obtained a number of *C. agilis* Koch (*C. serrulatus* Fischer), *C. albidus* Jurine and *C. vernalis* Fischer, along with ostracods, chironomid larvae of several species, planarians, nematodes, and a small snail, but these were never encountered in the plankton hauls in open water. Compare the plankton of White Lake, N. C. (Coker, '38). The available food for Entomostraca must consist of the smaller phytoplankters and bacteria, to which reference has been made in the preceding section. It is, then, of interest to examine the straining mechanism of the Entomostraca with regard to the fineness of the mesh. The strainer of *Daphnia* is understood to be formed by the combs of barbed setae on the third and fourth thoracic appendages (Storch, '22); that of *Diaphanosoma* by the somewhat similar combs on all thoracic appendages (Storch, '22, '25, '29a; Lochhead, '36) and that of *Diaptomus* by the comb on the second maxilla (Storch, '29b; Storch and Pfisterer, '25; Cannon, '28).

The measurements given in this paragraph and the accompanying table were made by Marjorie Carter and checked by the (senior) author. The barbs of the setae of the straining comb of *Diaphanosoma* and of the copepod, *Diaptomus leptopus*, were seen too faintly to get satisfactory measurements of the barbs themselves or of the spaces between barbs. The distances between barbs would, however, probably not far exceed two-thirds of the distance from center to center of barbs, which would be measured. The distances from center to center of the barbs of the setae of the outer (sweeping) lobe of the first maxilla of *Diaptomus* were found to be approximately 1.8 μ. The corresponding measurement for the inner lobe was 2.7 and for the inner (filtering) lobe of second maxilla was 2.6 μ. Measurements for *Daphnia* and *Diaphanosoma* are recorded in the following table.

Assuming that the food-capturing mechanism has been correctly interpreted, apparently the filtering webs of *Daphnia*, *Diaphanosoma* or *Diaptomus* might take any organism obtained in our centrifuge collections and there are doubtless few, if any, plankton bacteria that would not

*Measurements of meshes of straining combs of Daphnia and Diaphanosoma*

| | Measurements in μ | | |
|---|---|---|---|
| Parts or spaces measured | *Daphnia* | | *Diaphanosoma* |
| | (1) | (2) | |
| Length of carapace to base of spine | 1651.00 | 1530.00 | 1000.0 |
| Width of carapace | 1120.00 | 920.00 | 435.0 |
| Greatest length of seta on gnathobase of 3rd (or 4th) foot | 277.00 | 264.00 | |
| Length of barbs (setules) on seta | 5.27 | 3.72 | 9.0 |
| Distance from center to center of barbs | 1.03 | 1.03 | 1.1 |
| Width of barb | .34 | .34 | ? |
| Width of space between barbs | .68 | .68 | ? |

*Numbers of Entomostraca (by species) per cubic liter at several depths (July 22, 1937, midnight)*

| Species | Surface to 18 in. | 10 ft. | 20 ft. | 40 ft. |
|---|---|---|---|---|
| *Diaptomus leptopus* | 17.9 | 14.8 | .5 | 1.5 |
| *Diaphanosoma brachyurum* | 15.7 | 10.2 | — | 1.0 |
| *Daphnia pulex* | 24.5 | 6.8 | 1.0 | 2.5 |
| Total Entomostraca | 58.7 | 31.8 | 1.5 | 5.0 |

be held back by the filters of the Cladocera. The organisms observed in the alimentary tracts were small algae or algal colonies, the largest colony measured being one of *Sphaerocystis* with greatest diameter of 52 μ.

*Density of Populations.*—Attempts were made to determine the approximate density of population of the several larger plankters. Samples, taken at midnight with an improved Foerst water bottle of 2 liters capacity, were filtered through a Birge funnel. After the material had been killed by addition of alcohol, it was centrifuged and the concentrate pipetted out with 1 cc. of water and placed in a Rafter cell. The counts obtained divided by two gives the numbers of the several plankters per liter at the levels from which samples were taken. The figures must be regarded as giving only a very rough approximation to the actual mean numbers per liter. They clearly reflect the result of the nocturnal migration toward the surface.

## SUMMARY

1. Temperatures ranged from 26° (22–26°) C. at the surface to 8° C. at 16.8 m. (55 ft.) and down to 22 m. (73 ft.). The thermocline was between 4.5 m. and 9 m. (15 and 30 ft.).

2. The limnetic net plankton (taken with No. 10 bolting silk) of Mountain Lake in July, 1937, consisted almost exclusively of one copepod, two cladocerans, two rotifers, volvox and desmids. There were no *Cyclops* (although several species of this genus occurred littorally and amidst the vegetation on the bottom), and there were no plankton organisms of predatory habit.

3. These organisms occurred at all depths explored from surface to 60 ft. The general order of abundance was, by numbers per collection, *Notholca, Diaptomus, Diaphanosoma, Volvox, Daphnia, Conochilus,* Desmids. Of the Entomostraca, *Diaptomus* seemed most superficial in habit; *Daphnia* least so.

4. The nannoplankton comprised a number of species, but the bulk of it was a single species, *Dictyosphaeriopsis,* of the family Palmellaceae. The peak of abundance of the phytoplankton at the time of observation was in the lower third of the epilimnion.

5. The meshes of the straining combs of the Cladocera, at least, are fine enough to hold back, not only any alga, but doubtless also, any bacterium common in the lake water. The food supply available and availed of, as far as limited observations went, comprised the algae and a small amount of detritus.

6. Rough appraisals of the densities of population are given.

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# A STUDY OF THE DEPTH DISTRIBUTION OF CERTAIN NET PLANKTERS IN MOUNTAIN LAKE, VIRGINIA [1]

W. W. GROVER,[2] AND R. E. COKER[3]

This report is based upon 25 series of collections made at about 2:00 P.M. (12) and 12:00 M. (13) over a period extending from July 13 to August 1, 1937. Collections were made with a small closing net, Apstein style, the small (front) ring of the canvas cone having a clear opening of 95 mm., the net ring a diameter of 160 mm. The net was towed behind a rowboat over a course, determined by cross bearings at each end, and approximately 463 yds. (425 m.) long; the same course was followed in all hauls. As is indicated in the tables, hauls were made at the surface, 2 ft., 5 ft., 10 ft., 20 ft., 30 ft., 40 ft., 50 ft., and 60 ft. depths (225 collections in all). The depths recorded are approximations, based upon calibration of the line after measurements in the upper levels with maintenance of approximately consistent speed of the boat. Collections preserved immediately in 5 per cent formalin, were later concentrated to 10 ml. Counts were made in the laboratory with the use of a Sedgewick-Rafter Counting Cell, ten fields per cell being counted and the remainder of the cell scanned rapidly to check against any gross errors brought about by uneven distribution on the slide. In all, 1,920 separate counts were made, with record of 584,587 individuals or colonies of nineteen different species shown in table I.

Samples selected at random were recounted by others in order to check against a personal error. The divergen-

cies between these recounts and the original counts never exceeded 2½ per cent. The colonial Chlorophyceae were so predominantly of one kind (*Dictyosphaeriopsis*) that attempts were not made to distinguish species in the regular counts. Differential counts of these and a few other algae, not counted and recorded specifically, were run from time to time and always the relative proportions of the various species remained nearly constant (with deviations of the order of 3 per cent).

Table II gives the mean numbers of the several plankters found in one milliliter in afternoon and night respectively. Table III gives means of day and night collections (not shown in the graphs) for each depth.

The graphs, shown in figure 1 are modifications of the familiar area graph. The right and left halves in each case represent the distribution at the two different times of day at which collections were made (left for day, right for night). The vertical scale on the graphs represents depth in feet while the horizontal scale shows the number of organisms counted in one milliliter of the catch after concentration to 10 ml.; thus the total catch would amount to ten times the recorded figures or 5,845,870. The smaller numbers were used in order that diurnal migration might be more easily visualized in graphic representation.

Diversities in numbers for the several species at any given depth, which were noted from day to day, may well be attributed in part to irregularities in horizontal distribution and migration or drifting in horizontal directions. Künne ('26) describes streaking on the part of *Bosmina longirostris* O. F. M. and attributes this to the action of the wind. The authors believe that such irregularities are well offset by an adequate number of collec-

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TABLE I. *Summary of 225 collections of net plankters from Mountain Lake, showing number of each kind counted and percentages (by number) of whole catch* [2]

| | | No. counted (= 1/10 of collection) | Per cent by numbers |
|---|---|---|---|
| | *Zooplankton* | (rare) | |
| Protozoa: | | | |
|   *Dinobryon* | | | |
|   *Volvox aureus* Ehrenberg ⎱ | | 2,046 | 0.35 |
|   *V. terius* ⎰ | | | |
| Rotifera: | | | |
|   *Conochilus unicornis* Rousselet | | 126,890 | 21.70 |
|   *Notholca longispina* (Kellicott) | | 5,780 | 1.00 |
| Entomostraca: | | | |
|   *Diaptomus leptopus* Forbes | | 16,920 | 2.90 |
|   *Diaphanosoma brachyurum* (Liévin) | | 7,760 | 1.30 |
|   *Daphnia pulex* (de Geer) | | 6,660 | 1.10 |
| | *Phytoplankton* | | |
| Blue-green Algae: | | | |
|   *Anaebaena* sp. | | (few) | |
| Diatoms | | 862* | .15 |
| Desmids: | | | |
|   *Staurastrum limneticum* Schmidle | | 4,001 | 0.70 |
|   *S. curvatum* W. West | | 3,120* | .53 |
|   *Micrasterias rotata* (Grev.) Ralfs ⎱ | | 3,690 | 0.60 |
|   *M. americana* (Ehr.) Ralfs ⎰ | | | |
|   *Cosmarium dentatum* Wolle | | 311 | 0.06 |
| Protococcales: | | | |
|   *Dictyosphaeriopsis* sp. | | 401,333* | 68.63 |
|   *Crucigenia quadrata* Morren | | 2,299* | .39 |
|   *Planktosphaeria gelatinosa* G. M. Smith | | (few) | |
|   *Eremosphaera viridis* de Bary | | (few) | |
|   *Dimorphococcus lunatus* A. Braun | | 2,915* | .50 |
| | | | 99.91 |

* Computed on basis of differential counts mentioned on p. 199.
[2] Several species of *Cyclops* were found among the *Chara* of the shallower portions of the lake but none of these were collected by us in our nets during the period of study.

tions under different meteorological conditions.

The three Entomostraca—*Diaptomus leptopus* Forbes, *Diaphanosoma brachyurum* (Liévin), and *Daphnia pulex* (de Geer)—show a general conformity in migratory habit. In all three cases a strong upward migration at night was revealed. This was especially well shown in a 24-hour study of diurnal migrations of Entomostraca in the epilimnion of this lake carried out by others earlier in the same summer (Coker and Hayes, '40). The vertical migrations can hardly be attributed to anything other than a limited negative phototaxy, since the temperature changes are slight, affecting only the upper third of the epilimnion. Farran ('26) gives a record of diurnal migrations of plankters in the sea in which he finds the copepod population from the surface to 100 fathoms approximately doubled during the night by an upward migration of certain species.

The distributions of the two Cladocera, *Diaphanosoma brachyurum* and *Daphnia pulex*, show a distinct similarity in both diurnal and nocturnal distribution, while the calanoid copepod, *Diaptomus leptopus*, seems to tolerate a greater amount of light, as is indicated by its higher concentrations at about 5 ft. during the afternoon and at the surface at night. *Daphnia* seemed least tolerant of light. Only more extended study would show whether the indications of secondary peaks for *Diaptomus* and *Daphnia* in the afternoon at about 40 ft. are significant. The slight indication of a corresponding secondary peak for colonial Chlorophyceae at a little

higher level (30 ft.) is not strong enough to appear significant. We do not have detailed oxygen analyses but it is hardly possible that increased oxygen content in the depths would be sufficient to account for a rise in concentration of 160 per cent in the case of *D. pulex* (from 24 per catch at 30 ft. to 62 at 40 ft.). Schomer ('34), in work on northern lakes, has shown that, even in the very clear lakes, the

TABLE II. *Vertical distribution of plankton organisms in Mountain Lake, Virginia, recording mean nos. per milliliter examined for daily collections, July 21 to August 1, 1937, made at about 2 P.M. (14 o'clock) (upper figure in each case) and for corresponding collections made about midnight (lower figure). Multiply each figure by 10 for number collected. Heavy type indicates peaks of abundance; italics indicate secondary peaks.*

| Organism | Surface | 2 ft. | 5 ft. | 10 ft. | 20 ft. | 30 ft. | 40 ft. | 50 ft. | 60 ft. |
|---|---|---|---|---|---|---|---|---|---|
| *Diaptomus* | 67 | 337 | **498** | 257 | 177 | 68 | *80* | 56 | 26 |
|  | **956** | 447 | 265 | 160 | 43 | 41 | *49* | 28 | 26 |
| *Diaphanosoma* | *18* | 2 | 102 | **220** | 194 | 33 | 18 | 2 | none |
|  | 299 | **357** | 246 | 129 | 25 | 8 | 1 | none | none |
| *Daphnia* | 1 | none | 15 | **182** | 105 | 24 | *62* | 10 | *33* |
|  | 207 | 221 | **266** | 85 | 33 | 27 | 15 | 21 | *26* |
| Total Entomostraca | 86 | 339 | 615 | **659** | 476 | 125 | *160* | 68 | 59 |
|  | **1,462** | 1,025 | 777 | 374 | 101 | 76 | 65 | 49 | 52 |
| *Conochilus* | *1,216* | 54 | 1,829 | **2,523** | 996 | 182 | 110 | 35 | *163* |
|  | 3,876 | **6,307** | 4,228 | 2,754 | 906 | 106 | 39 | 19 | none |
| *Notholca* | *53* | 18 | 29 | 25 | **201** | 73 | 24 | 17 | *26* |
|  | *41* | 39 | 18 | 87 | **296** | 73 | 22 | *69* | 48 |
| *Volvox* | *37* | none | 1 | 27 | **73** | 37 | 16 | 3 | *24* |
|  | 4 | 8 | * | 18 | **40** | 36 | 26 | 7 | 6 |
| *Staurastrum* | *136* | 49 | 41 | 43 | **68** | 20 | *30* | 1 | none |
|  | **80** | 31 | 47 | *65* | 56 | 37 | 22 | 28 | 4 |
| *Micrasterias* | 77 | 51 | 21 | **70** | 62 | 18 | 10 | * | *44* |
|  | **89** | 69 | 57 | *67* | 50 | 13 | 13 | 4 | *22* |
| *Cosmarium* | 2 | none | 5 | 2 | none | none | none | none | none |
|  | 9 | none | 1 | **18** | 15 | 3 | none | 7 | none |
| Colonial Chlorophyceae | *1,508* | 538 | 2,115 | **6,622** | 5,064 | 4,514 | 4,940 | 2,674 | 1,168 |
|  | **9,964** | 8,434 | 7,295 | 7,159 | 5,893 | *6,231* | 3,777 | 2,535 | 1,250 |

\* Present in small numbers in the collection, but not found in one milliliter counted.

TABLE III. *Mean distribution (day and night), Mountain Lake, Virginia, June 21–Aug. 1, incl., 1937. Heavy type indicates peaks of abundance; italics indicate secondary peaks.*

| Organism | Surface | 2 ft. | 5 ft. | 10 ft. | 20 ft. | 30 ft. | 40 ft. | 50 ft. | 60 ft. |
|---|---|---|---|---|---|---|---|---|---|
| *Diaptomus* . | **511** | 392 | 281 | 209 | 110 | 55 | 64 | 42 | 26 |
| *Diaphanosoma* | 108 | **178** | 174 | 175 | 109 | 21 | 10 | 1 | none |
| *Daphnia* | 104 | 110 | **140** | 133 | 69 | 25 | 39 | 15 | 29 |
| Total Entomostraca | **723** | 680 | 595 | 517 | 288 | 101 | 113 | 58 | 55 |
| *Conochilus* | 2,546 | **3,180** | 3,028 | 2,639 | 951 | 144 | 75 | 27 | 81 |
| *Notholca* | *47* | 28 | 23 | 56 | **248** | 73 | 23 | *43* | 37 |
| *Volvox* | *20* | 4 | 0.7 | 37 | **56** | 36 | 21 | 5 | *15* |
| *Staurastrum* | **116** | 40 | 44 | 54 | *62* | 28 | 26 | 15 | 15 |
| *Micrasterias* | **83** | 60 | 39 | *69* | 56 | 16 | 11 | 2 | *33* |
| *Cosmarium* | 5 | none | 3 | **10** | 8 | 2 | none | 3 | none |
| Colonial Chlorophyceae | *5,736* | 4,486 | 4,705 | **6,891** | *6,891* | 5,373 | 4,358 | 2,604 | 1,209 |
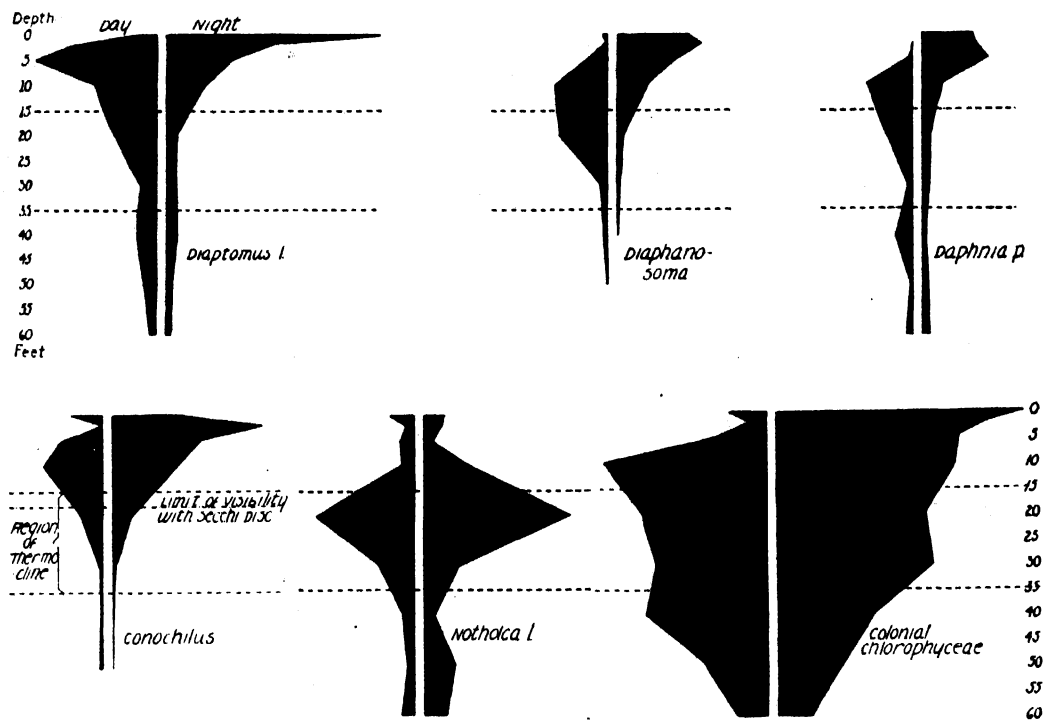
FIG. 1. Illustrating bathymetric distribution of principal plankters of Mountain Lake (July 21 to August 1) by day, *left*, and night, *right*. Equivalent scale used for Entomostraca (in upper tier). Relative to the Entomostraca, *Conochilus* and colonial Chlorophyceae (lower tier) were 10 times as abundant (by number) as the graphs indicate, *Notholca* half as abundant. Depth in feet (0–60) indicated vertically.

compensation point (for liberation and consumption of oxygen by algae) lies somewhere between 10 and 15 m. (33 and 49 ft.). In view of the lower excess of oxygen produced over oxygen consumed, even a substantial increase in the algal population (which is not found) would not be expected to account indirectly for increased animal population on the basis of oxygen production. Temperature is hardly to be considered as a determining influence in this case, since the level of 40 ft. depth is well within the hypolimnion.

A significant inference from the data of diurnal migrations of Entomostraca in Mountain Lake is this—that, particularly with *Diaptomus*, we seem to have to do not so much with a movement of whole populations as with distinct shifts in centers or levels of concentration of populations (suggestive of considerable individuality in response to the conditions

controlling the migrations). Juday ('04) cites many instances where entomostracan species were "absent from the upper 5 meters in the daytime," etc. In Mountain Lake only *Daphnia* actually disappeared during the daytime from the upper 2 or 3 ft. *Diaphanosoma* were indeed few above 5 ft., but *Diaptomus* was present in significant numbers in the upper few inches in the daytime although more than ten times as abundant there during the night. To quote Tressler ('39) in his comment on Langford's ('38) experiments in respect to vertical movements of certain Entomostraca in a laboratory aquarium with changes of temperature and of content: "Some individuals remained under conditions from which others migrated."

Diurnal migrations, similar to those of the Entomostraca are revealed for no other organism on our list except the colonial rotifer, *Conochilus unicornis*

Rousselet, for which a rise for the greater part of the population toward the surface at night is well marked; an increased concentration at 60 ft. during the afternoon is noted. It would be useless, however, to attempt to analyze the movements of this species on the basis of our data, since it is obvious that so large a part of the population found at night is quite unaccounted for in the daytime records.

The other common rotifer, *Notholca longispina* (Kellicott), shows, both day and night, a prominent primary peak of abundance at 20 ft., with minor secondary peaks at the surface and at 50 or 60 ft.

The records for the desmids, *Micrasterias* and *Staurastrum,* and the protozoan, *Volvox,* offer no indication of diurnal migrations in a vertical direction. The desmid, *Cosmarium,* was encountered too infrequently for consideration.

The data for colonial Chlorophyceae are not so easily analyzed. At first glance the records seem to indicate a remarkable upward migration at night—until we observe that actually about as many of these algae were found below 20 ft. at night as during the day. The great nocturnal population of the upper 10 ft. is simply not accounted for by comparison with the day collection. This is not quite so evident for the rotifer, *Conochilus,* where we have nevertheless a disproportionately large increase to be

accounted for with respect to the nocturnal population in the epilimnion. With respect to all three species of the Entomostraca, on the other hand, we find by night a notable decrease in the deeper populations although, again, there are, at least in the case of the two cladoceran species, nocturnal increases in population not fully accounted for by withdrawals from the deeper layers. The summaries of distribution by larger zones for certain species, as given in table IV, illustrate clearly the anomalies just discussed.

For the apparent discrepancies, several possible explanations might be considered. (1) There might have been some inadvertent difference in technique of collecting by night and by day; to the authors this does not seem likely. (2) Because of irregularities in horizontal distribution and random horizontal migration, the collections may not have been representative of any general plan of distribution and migration. Against this it may be said: that the records are based not on two or three collections but on collections made on 15 days; that the evidence of daily losses of population in the hypolimnion in cases of most of the actively motile organisms is too clear and consistent to be explained by chance or technical errors; and that a very similar story of diurnal migration was revealed by a series of collections made at 6-hour in-

TABLE IV. *Showing distribution of chief plankters by larger zones (condensation of table II)*

|  |  | S.–5 ft. | 10–20 ft. | 30–60 ft. | Total |
|---|---|---|---|---|---|
| *Diaptomus* | Day | 902 | 434 | 230 | 1,566 |
|  | Night | 1,668 | 203 | 144 | 2,015 |
| *Diaphanosoma* | Day | 122 | 414 | 53 | 589 |
|  | Night | 902 | 154 | 9 | 1,065 |
| *Daphnia* | Day | 16 | 287 | 129 | 432 |
|  | Night | 694 | 118 | 89 | 901 |
| *Conochilus* | Day | 3,099 | 3,519 | 490 | 7,108 |
|  | Night | 14,411 | 3,660 | 164 | 18,235 |
| *Notholca* | Day | 100 | 226 | 140 | 466 |
|  | Night | 98 | 383 | 212 | 693 |
| Colonial Chlorophyceae | Day | 4,161 | 11,686 | 13,296 | 29,143 |
|  | Night | 25,693 | 13,052 | 13,793 | 52,538 |

tervals earlier in the summer (Coker and Hayes, '40). (3) The results may be confused by a regular diurnal migration in a more or less horizontal direction. The lake is not very wide, and the place of collection was hardly a hundred yards distant from the shaded shores. The one abundant plankton organism whose increased surface population at night could most nearly be accounted for by migration from the deeper waters was, it may be noted, the more strictly *limnetic* entomostracan, *Diaptomus leptopus* [3] (see table IV). Southern and Gardiner ('26) found night collections much larger than day collections and believed the difference was due to the ability of plankton organisms to see and avoid the net. Certainly, however, such an explanation would not be applicable to Chlorophyceae and doubtfully to the rotifers.

In previous years, *Dinobryon* has been known to appear in sufficiently large numbers to give a muddy appearance to the lake and to cut the transparency from one-third to one-half.[4] In 1937 only one colony of *Dinobryon* was found during the entire period of collecting beginning in the last days of June and continuing some time after the period of quantitative study which ended August 1. No Protozoa other than *Dinobryon* and *Volvox* were collected in our nets from the limnetic region, although a number of others were found in the littoral regions by Robert in 1937.

CONCLUSIONS

1. Virtually all species (or groups) showed a lack of uniformity in vertical distribution with notable peaks of abundance at particular levels and with one or more subordinate peaks at other levels.

2. The zooplankton is concentrated

[3] There remains, of course, the possibility that there are some critical peak levels that were not sampled in this study. Such for example would be the very bottom waters below our lowest collection level.

[4] Unpublished records in the possession of the Mountain Lake Biological Station, Graduate School, University of Virginia.

largely in the epilimnion and in the extreme upper portion of the thermocline, the levels of maxima shifting upward by night.

3. The active animals, *Diaptomus, Diaphanosoma* and *Daphnia* had at night, as compared with the day, decidedly decreased populations in the deeper waters from 10 to 60 ft., a roughly corresponding increase in upper levels for *Diaptomus* and a much more than corresponding increase for *Diaphanosoma* and *Daphnia*. A confusing cross (horizontal) migration is suggested for the two latter species.

4. Only *Daphnia* seemed actually to disappear in the daytime from the upper 2 or 3 ft. By day or night levels of greatest population density were not far below the surface. *Diaptomus* tended to crowd to the very surface at night.

5. As regards the rotifers, there was no positive evidence of diurnal migration by *Notholca*, but some evidence, in the records for 30 ft. and lower, of a withdrawal of *Conochilus* from the hypolimnion at night. On the other hand, there is recorded a more than 4-fold increase by night in the population of this species in the upper 10 ft. The origin of a large part of the increased upper-level population, which is more than can be accounted for by vertical migration, is problematic.

6. Although *Micrasterias, Staurastrum* and *Volvox* are not uniformly distributed, the peak of abundance for the two desmids being close to the surface and that for *Volvox* at 20 ft. (upper part of thermocline), there were no notable differences in day and night records.

7. The colonial Chlorophyceae, chiefly *Dictyosphaeriopsis*, had a much more even vertical distribution, occurring in significant numbers as low as 30 and 40 ft., but with concentration by day in the lower epilimnion (primarily), the thermocline, and the upper hypolimnion and by night near the surface and throughout the epilimnion. They occurred in approximately equal numbers by day and by night at levels from 10 to 60 ft. An explanation for the 6-fold increase by

night in numbers in the upper 5 ft. must be sought in causes other than vertical migration.

8. The need for a study of possible diurnal horizontal migrations is indicated.

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# PLANT SUCCESSION IN THE LARREA–FLOURENSIA CLIMAX

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The Larrea-Flourensia Desert Scrub is a widespread and relatively homogeneous community common to the central continental areas of the southwestern United States and northern Mexico. Its structure, ecological adaptations and responses, and its significance in the classification of plant communities are vastly different from those of other North American communities and particularly those of the East. The significance in classification has largely been overlooked. The present paper is intended to present the problem in the light of investigations carried out on a selected site in western Texas. Study was begun in 1931 while the author was engaged in other botanical work in that area, was continued in 1932 and 1933, and was reviewed in 1939. The successively denuded and covered Tornilla Clay beds were chosen for study because of their extremely unfavorable conditions for plant growth. Depletion of surface soil overlying them is disturbance in high degree.

## THE TORNILLA CLAY AREA

The Tornilla Clay beds were described by Udden ('07) on Tornilla Creek, a minor tributary of the Rio Grande flowing past the Chisos Mountains in Brewster County, Texas. The clay beds occur extensively adjoining the creek to the north and northeast of the mountains and are exposed over smaller areas in lesser erosion systems west of the mountains. The beds are characteristically overlaid by a layer of rubble and sandy soil which forms the desert plain adjacent to the mountains. Erosion of the surface layer exposes the clay which is highly resistant to weathering and persists in the form of rounded hillocks.

The physical characters of Tornilla Clay are very striking. The color ranges from light gray through blue, maroon,

purple, and yellow. The texture is exceedingly fine and dust-like, but the particles adhere in lumps ranging from the size of a pea in weathered clay to huge matrices comprising virgin beds. The weathered lumps occupy the surface two or three inches of the exposed hillocks, and occasionally narrow fissures develop to a depth of several feet, and water runs freely through them as is evidenced by minute deposits of iron along the cleavage planes. The very fine texture of the substratum allows practically no penetration of water. On a roadway where traffic had pulverized even the weathered lumps, a one-inch rain failed to penetrate beyond a depth of half an inch. Similarly, although the formation of lumps and fissures allows the penetration of water *between* the masses, little if any moisture penetrates the masses themselves. The clay is occasionally alternated with or adulterated by layers of sandstone which, upon mixing by erosion, serve to mitigate the strict imperviousness of the clay.

Drying is very rapid with the result that scarcely a half dozen days in the year does the clay contain sufficient moisture to support plant growth. The extremely unfavorable conditions for plant growth on the bare clay is clearly indicated by the total lack of any plants on such areas.

Erosion in Tornilla Clay areas follows a very definite pattern. The sandy soil of the desert plain and the outwash of detritus from the foothills and mountain slopes is first washed off the clay beds. The clay rounds up to form hemispheric or cone-like hillocks. These are very slowly eroded and mixed with the sandy and gravelly detritus from above to form a second desert plain at a lower level; that is, on the floor of the stream-valley. Low hillocks of pure clay are sometimes coveret thinly with gravel washed from the tops of adjacent higher hillocks. Thus

the history of any given point may begin with sandy or gravelly desert plain, proceed through various successions of pure clay, mixed clay and gravel, pure clay again, and finally upon reaching the base level of the erosion system, a thorough mixture of clay, sand, and gravel not much different from the original desert plain.

NATURE OF THE SURROUNDING DESERT

The low altitude (2,800 to 3,500 feet), flat topography, low rainfall (about 10 inches annually), abundant insolation, and resultant high temperatures and high rate of evaporation combine to make the plain about the Chisos Mountains highly xeric. This condition is markedly reflected in the climax vegetation of the area, which consists of Larrea-Flourensia Desert Scrub. This is the Creosote Bush or Southern Desert Shrub of Shantz and Zon ('24), the Chihuahuan Desert of Shreve ('39), and very like the Central Plateau Desert Scrub in Nuevo Leon described by the present author in an earlier paper ('39). In the Chisos area the desert scrub agrees with Shreve's description of the Chihuahuan Desert in that it is

characterized chiefly by *Larrea tridentata* with which are associated *Prosopis chilensis* where the soil is deep and *Flourensia cernua* where the soil is thin. Thin soil is characteristic of the Chisos plain, and therefore Larrea-Flourensia Desert Scrub is relatively constant. (See fig. 1.)

Whitfield and Beutner ('38) have questioned the climax condition of the Larrea-Flourensia Desert Scrub. They included wide areas of this type in the Desert Plains Grassland and proposed that overgrazing has resulted in the replacement of grasses by shrubs. This subject is being treated separately in another paper, and certain areas of Larrea-Flourensia are here regarded as conclusively climax regardless of whatever fluctuations may be demonstrated to take place within the ecotones between Larrea-Flourensia Desert Scrub and Desert Plains Grassland.

Characteristically associated in the Larrea-Flourensia Desert Scrub on the flats are the following plants named approximately in the order of decreasing importance: *Larrea tridentata* (DC.) Cov., *Flourensia cernua* DC., *Porlieria angustifolia* Gray, *Agave lechuguilla*



FIG. 1. Typical Larrea-Flourensia Desert Scrub with *Agave, Fouquieria, Porlieria, Prosopis,* etc. on sandy, gravelly soil overlying a bed of Tornilla Clay.

Torr., *Prosopis chilensis* (Mol.) Stuntze, *Fouquieria splendens* Engelm., *Zizyphus lycioides* Gray, *Acacia constricta* Benth., *Opuntia leptocaulis* DC., *Dasylirion leiophyllum* Engelm., *Acacia Greggii* Gray, *Yucca baccata* Torr., *Koeberlinia spinosa* Zucc., *Krameria grayi* Rose & Painter, *Opuntia macrocentra* Engelm., *Echinocereus stramineus* (Engelm.) Rümpler, *Ephedra antisyphilitica* Meyer, *Yucca elata* Engelm., *Atriplex canescens* (Pursh) Nutt., *Porophyllum scoparium* Gray, *Leucophyllum texanum* Benth., *Nolina erumpens* (Torr.) Wats., *Menodora scabra* Gray, *Cevallia sinuata* Lag., *Aristida glauca* (Nees) Walp., *Bouteloua breviseta* Vasey, *Hilaria mutica* (Buckl.) Benth., *Sporobolus airoides* (Torr.) Torr., *Croton neomexicanus* Muell.-Arg., various Compositae and Nyctaginaceae.

The vegetation has the familiar aspect of desert; that is, the plant growth occupies a very low percentage of the soil surface and is composed of widely spaced shrubs with very sparsely interspersed herbs. Only occasionally does *Agave lechuguilla* form a dense cover. It is not meant to imply that the Larrea-Flourensia cover with its associated species is a homogeneous community. In some rocky areas of limited extent *Dasylirion* and *Fouquieria* become dominant; in others *Larrea* and *Acacia constricta* form an exceedingly sparse cover; still others support a somewhat more luxuriant growth composed to greater or lesser extent of all the species listed above. Certain species, such as *Dasylirion leiophyllum*, *Yucca elata*, *Koeberlinia spinosa*, *Zizyphus lycioides*, *Porophyllum scoparium*, *Hilaria mutica*, and *Sporobolus airoides*, reach their best development on somewhat eroded rocky slopes.

## PLANT SUCCESSION IN THE EROSION CYCLE

As the pervious surface soil is washed off the underlying clay beds, the less xeric of the plant species rapidly disappear leaving behind only those capable of
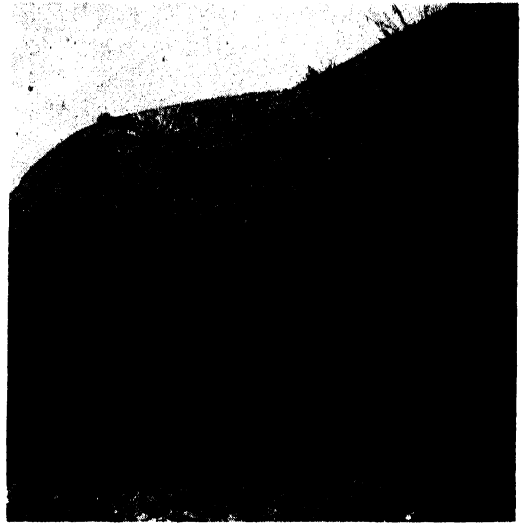


FIG. 2. Remnants of the desert scrub consisting of *Fouquieria, Agave, Nolina, Sporobolus,* and *Hilaria* on depleted soil overlying impervious clay.

persisting on a few inches or a foot of suitable soil. A few stunted individuals of *Larrea, Agave, Nolina, Ephedra, Fouquieria, Dasylirion, Hilaria,* and *Sporobolus* form the sparse cover on such depleted soil. (See fig. 2.) As the soil is still further removed, the grasses alone remain, together with an occasional shrub whose roots have penetrated one of the few deep fissures in the underlying im-
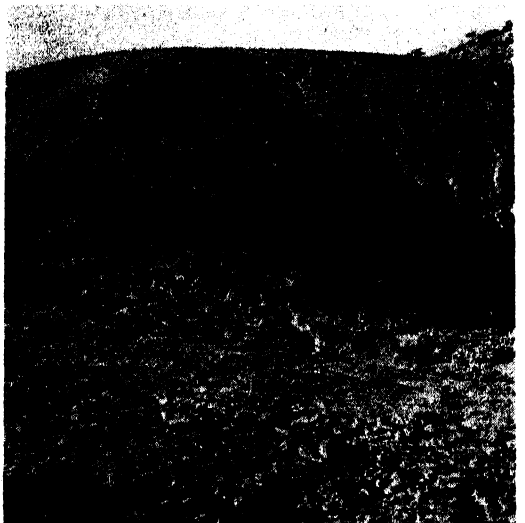


FIG. 3. *Sporobolus* and *Hilaria* relict on the last remnant of soil on a clay hillock.

FIG. 4. A bare clay hillock.

pervious clay. (See fig. 3.) When the last vestige of soil has been removed from the clay, no plant growth is in evidence. (See fig. 4.)

Following a period of weathering of the clay and admixture in the surface few inches of sand and gravel washed down from the adjoining desert plain, the soil is again capable of supporting the more xeric and more shallow-rooted species. *Hilaria* and *Sporobolus* are the first invaders. As the rubble becomes deeper, especially in tiny ravines between the clay hillocks, some of the shrub species enter. Among these *Acacia greggii, Agave,* and *Prosopis* are the first. (See fig. 5.)



FIG. 5. *Acacia greggii* and *Sporobolus* on a catchment of gravel and sand in a clay ravine.

Subsequent erosion may again denude the area, but a second admixture of pervious soil results in the same succession. When the clay is finally well mixed with gravel, all the original desert species are able to enter. However, as a result of the uneven topography and the immature soil, the vegetation takes on the appearance of the usual ravine growth with an abundance of *Zizyphus, Koeberlinia, Porophyllum,* and grasses. As base level is approached and the topography becomes less broken *Larrea, Prosopis, Flourensia, Acacia constricta, Krameria,* and others sparsely dominate the area, and the dense thickets of *Zizyphus,* etc. are dissipated to a mere scattering. At the early base level stage the area is essentially desert plain, but the soil contains so high a percentage of the sterile and poorly pervious clay that the characteristically scattered scrub vegetation of the desert plain is here even more sparse. (See fig. 6.) Eventually the soil becomes more thoroughly weathered and matures to form typical desert plain, free from the adverse effects of raw clay and equal in vegetation to the original desert plain.

To summarize, the denuding of clay and its subsequent mixture with pervious soil carries an area through the following stages of retrogressive and progressive succession:

1. Original climax Larrea-Flourensia Desert Scrub with which are associated many xeric shrub and herb species, occupying unbroken sandy or gravelly soil.

2. Sparse remnants of the more xeric shrubs and shallow-rooted grasses on soil a foot or less in depth above the impervious clay.

3. Last relicts of grasses on shallow remnants of soil on denuded clay.

4. No plant growth at all on bare, impervious clay.

5. Shallow-rooted grasses, the first invaders of weathered clay with a thin cover of washed-in sand and rubble.

6. Sparse shrubs tolerant of soil a foot deep on clay.
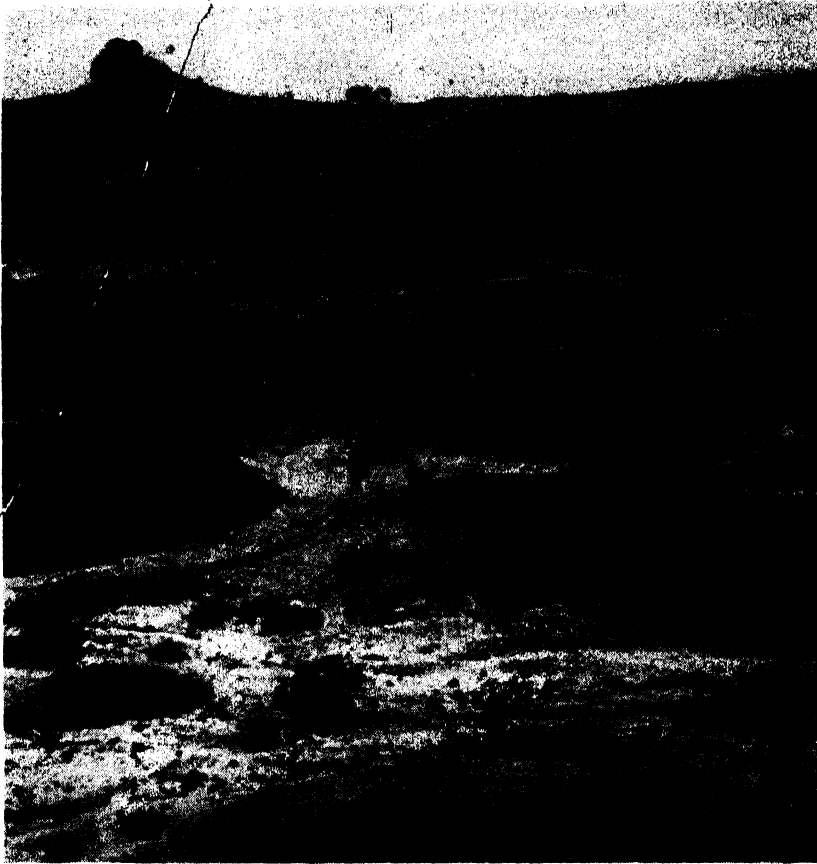
Fig. 6. An immature desert plain on the base level of the ersoion system bearing very sparse desert scrub vegetation.

7. Dense shrubs of all species on well covered clay of rough topography.

8. Sparse representation of Larrea-Flourensia Desert Scrub on the new plain of immature soil at the base level of the erosion system.

9. Typical climax Larrea-Flourensia Desert Scrub on base level plains of mature soil.

## SIGNIFICANCE OF TORNILLA CLAY SUCCESSION

Weaver and Clements ('29) have attached great importance to plant succession as a means of classifying vegetation. All those areas bearing vegetation incompatible with the designated climax types have been considered seral stages. Were the principle left in that form, it would be difficult to criticize the succes-

sional method of vegetation classification. However, the concept of climax has been made so narrow and its application so broad that very little of the earth's surface may be said to be in climax condition. Many of the areas considered by some ecologists to be climax are held by others to be seral stages of other climaxes.

On the other hand, there are some areas which have no seral stages. A notable example of this is the Larrea-Flourensia Desert Scrub. In the succession described above, this vegetation type is exposed to the most extreme disturbance, but the result is not a succession in the sense of Weaver and Clements. No species foreign to the vegetation type invade the denuded area, although the close proximity of the Chisos Mountains (one to three miles) would insure the availability of disseminules of an abundance of

species. Only species comprising the original desert scrub are found in the disturbed areas, and as soon as the soil is capable of supporting a cover of plants, the original vegetation type appears in scarcely modified form. In the strict sense of the word there is no succession in Larrea-Flourensia Desert Scrub.

## CONCEPT OF CLIMAX COMMUNITIES

The concept of climaxes, like the species concept, has as many forms as it has interpreters. Those who consider the Oak-Hickory forest of the East as a single climax association with various seral stages stand in direct opposition to those who consider the several stages as legitimate separate Oak-Hickory climax associations. But regardless of how finely one splits the concept or how broadly it is interpreted, the concept is not compatible with the condition of the Larrea-Flourensia Desert Scrub. Since the principle of plant succession was developed in and applied to the vegetation of the eastern portions of the United States, it is not remarkable that its application in southwestern and other distant areas has proven difficult and often impossible. Seral stages have been demonstrated for each major climax type in the East. The absence of such stages in the desert scrub zones is of great significance in indicating the lack of relationship of the desert climax to the various more mesic climaxes. It is obvious that the desert type is more stable, more thoroughly attuned to its climatic environment, and more permanently fixed than are the precariously balanced forest types of the East. In other words, the desert is much more thoroughly climactic than are the other types.

Since the word "climax" as it is used in ecological terminology is a superlative, to speak of one condition as "more climactic" than another is erroneous. One is therefore faced with the necessity of choosing between erroneous usage and erroneous classification unless vast changes in terminology are to be made. In order to avoid too violent change in terminology

and yet to distinguish between those vegetation types which are relatively unstable climaxes and those, such as Larrea-Flourensia Desert Scrub, which are highly stable, it is here proposed that the latter be called *super-climax*. To this class of vegetation types belong all those communities which, upon being profoundly disturbed, are replaced by their original component species and thereby directly form a community ecologically (as well as floristically) equal to the original vegetation. Only those communities which are dependent solely upon climate for their stability are capable of such auto-succession. If soil changes or other disturbances invoke succession of a different vegetation type, the community is not stable, climate is not the determining factor, and the community cannot be called a super-climax.

At least one latitudinal zone on the earth's surface has such extreme climate that its vegetation is determined solely by the climate. This is the area occupied by arctic tundra. Extreme tundra consists of relatively few species, all of similar growth form, and is auto-successive because of rigorous climatic conditions. Griggs ('36), in discussing the vegetation of a subarctic (tension zone) area of Alaska, points out that even there competition is not a factor in community composition because of the rigorousness of the climate. The still more extreme conditions of truly arctic areas would greatly lessen the number of species able to survive and thus eliminate competition and succession. This latter condition was described (unpublished) by Mr. C. O. Erlanson (Bureau of Plant Industry) as occurring in the more extremely rigorous parts of Greenland.

In the temperate zones those areas located in the interiors of large continental masses have a sufficiently extreme climate to produce a super-climax. It will be noted that in every continental mass of considerable size with plains at low elevations occupying a central position, those central plains are desert. Local rigorous

climates may be found near the periphery of a continent, such as tundras on high peaks, deserts to the lee of coastal mountain ranges, etc. Such topographically induced climates support the equivalents of super-climaxes only so long as the topography favors the existence of the climates. Pending great physical changes, they are as stable as continental desert and had best be considered super-climaxes.

More mesic and more temperate climates favor several mutually exclusive growth forms which alternate as other physical conditions change, aspen succeeding hemlock or pine, dicot herbs succeeding grass, oak succeeding pine, etc. Mesic conditions and moderate temperatures are not limiting factors.

Transition zones between super-climaxes and less stable areas occur just as they do between climaxes and seral stages. The equatorward border of polar tundra and the periphery of a desert are both tension zones. These in no way reflect on the stability of more centrally located parts of the super-climaxes.

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# SOME OBSERVATIONS ON THE CONCEPT OF SPECIES SENESCENCE [1]

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There are several references in the literature to the concept of species senescence in which populations of plants are described as old, weak, conservative, and unaggressive, as distinguished f r o m young species populations which are said to be strong, competitive, dominating, vigorous. The population conditions are described in terms which commonly are also used to describe individual organisms when they are old or young.

The concept of species senescence usually is applied to local, and presumably relic, colonies of plants which belong to floral groups of a type called "epibiotic" (Ridley, '30) or "allogenous" (Marie-Victorin, '38).

For example, we read in writings on the Cordilleran elements found in the flora of the Gulf of St. Lawrence region (Fernald, '25), "This failure of the plants of the unglaciated spots to extend their ranges into closely adjacent areas which, upon the melting of the Labrador sheet, became open territory ready for invasion is interpreted as a further evidence of the antiquity of these plants; at the close of the Pleistocene they were already too old and conservative to pioneer, although they were able to linger as localized relics in their special undisturbed crannies and pockets." In contrast, later on, we read, "The younger Arctic flora which made its way south, in eastern America and in Europe at least, coincidentally with the advance of the comparatively recent Labradorean or Wisconsin and the later Baltic ice-sheets, has not yet had time to set off local species . . . . and far from being the rarest and most retiring of relics on our mountains, these young plants, like the young of the human species, are aggressive, dominating and from mere

youthful vigor inclined to crowd out the survivors of a more ancient cycle whose territory they had only recently invaded." (See also, Fernald, '29.)

From the interesting discussion of botanical problems of eastern Canada by Marie-Victorin ('38) we can abstract several comments related to the question of species senescence. He says, "We are naturally led to infer that our living allogenous flora is a survivor of an important and now largely extinct flora cornered on the nunataks during the Wisconsin glaciation . . . . We picture that since forty-odd thousand years, perhaps, they wage a losing fight against the sturdy northern conifers and their natural ecological associates . . . . It s e e m s too much for them. Through ecological pressure or through the failure of some essential biological processes, intrinsic or extrinsic, the old species have already surrendered most of the ground. They are mostly local, some of them extremely so, being confined to one mountain-top, or to one secluded cove by the seashore."

A few paragraphs later: "A last word on a point that might have been raised at the very outset of this study. Is the conception of a senescent preglacial or interglacial flora, vanishing gradually from northeastern America, defensible on biological grounds? Are there really such things as senescent species, and senescent floras in the present world?"

"I have often caught smiles on the lips of my biological auditors, when indulging in such anthropomorphic utterances. But I do not think we can escape a more or less guarded admission of this kind, if we look at the facts without bias . . . . Such extremely local plants as *Cirsium minganense* certainly seem to be doomed. If we could prove with reasonable certainty that these forms are disappearing because

they are 'old' to the point that some essential mechanism has ceased to be functional, we could open a new chapter of auto-ecology, and grasp at least one of the negative aspects of evolution."

Professor Marie-Victorin then adds, "But we are now in possession of a first series of experimental data in connection with the 'health' of the allogenous units of eastern North America. A certain number of the rarest relics and endemics have been grown for the last two years in the Montreal Botanical Garden. Quite unexpectedly they are very successful . . . . What of it? Since there does not seem to be anything fundamentally senescent or lethal in the plants themselves, we are naturally led to concede the senescent condition to the allogenous flora as a whole."

There may be occasions when our thinking on biological problems is facilitated by personifying our concepts or by individualizing our approach to species population problems. Of this I am doubtful, but in the case of epibiotic floras it seems unnecessary and obscure to employ the anthropomorphism of the concept of species senescence. There appear to be other, and more satisfactory explanations.

Let us consider two bodies of facts in this connection. First, each organism has a certain ecological amplitude. By this expression it is meant that an organism's range of tolerance for different intensities of a certain environmental factor is limited. Some plants have a wider range of tolerance for, let us say, hydrogen-ion concentration of the substratum, than do certain other plants. The plants which compose a species have approximately similar ecological amplitudes. Thus it is that we can speak of the pH tolerance of a species and call some species calcicoles and others oxylicoles (calciphiles and calciphobes). Also, it appears that genetic factors control the physiological attributes of a plant just as truly as they control the morphological attributes of the same plant. Of course, physiological adjustments by a plant are possible, just as tis-

sue plasticity results in greater or lesser xeromorphism according to the environment. But, and this point is important to the thesis, the capacity of a plant to vary physiologically is strictly within the inherited limits just as truly as the plant is limited morphologically by its inheritance. A plant inherits a certain ecological amplitude.

The second fact we need to consider is that species populations in nature are heterozygous and consist of tremendous numbers of biotypes. Within all large, wide-ranging, species populations there are geographical partial-populations which differ genetically from other partial-populations. E v o l u t i o n takes place through the isolation by one means or another of a portion of the large species population. No isolation, no speciation.

In wide-ranging species populations mere distance constitutes a type of isolation and marginal or other portions of a population are frequently recognizable as varieties or subspecies without the development of any conspicuous discontinuity. Furthermore, these marginal portions of a species population are relatively less heterozygous than the species as a whole.

We have thus set the stage for at least one explanation of the phenomenon which passes as species senescence. The so-called Cordilleran species which have been described as composing the epibiotic flora of the Gaspé and similar regions are represented in the East by descendants from mere fragments, peripheral fragments, of the original populations which crossed the continent in intra- or pre-Pleistocene times. Although many of the eastern populations are classified as identical taxonomically with the western populations of the species, there are numerous pairs of vicarious varieties and vicarious species.

The common lack of colonizing ability of the eastern epibiotics would seem to be due to their relatively greater homozygosity and consequent narrower ecological amplitudes; ecological amplitudes which are at one and the same time nar-

rower than those of their western coun-
terparts, and narrower than those of the
characteristic dominant acid soil flora of
the region.

The observations of Anderson ('36)
are to the point. "The variation within
*Iris setosa* var. *canadensis* seems particu-
larly instructive in the light of its recent
history. It is typical of those species
whose once continuous range across
northern North America was reduced to
the northeastern and northwestern edges
of the continent by the Pleistocene ice.
In Alaska a large central region was left
unglaciated; around the Gulf of St. Law-
rence, on the other hand, the plant ref-
uges in glacial times were little more than
rocky nunataks rising above the ice. The
results on the two sets of irises are just
what the geneticist might predict. Even
from the few specimens which are avail-
able in herbaria one can see that the *Iris
setosae* of Alaska are a varied assemblage
. . . . The irises of eastern Canada pre-
sent a very different picture . . . . Com-
pared to the millions of irises which might
well have continued to live in Alaska dur-
ing the ice age, those of the St. Lawrence
were a mere handful. From that hand-
ful must have descended the millions upon
millions of irises which now carpet the
meadows and shores of that region in
early summer. Compared with our other
American blue flags they are a singularly
invariable lot . . . . This conservatism of
*Iris setosa* var. *canadensis* is distinctive of
most of the glacial endemics (or near en-
demics) of the region around the Gulf
St. Lawrence. . . . In the case of *Iris
setosa* var. *canadensis* the invariability
cannot be a direct effect of time, for the
highly variable irises of Alaska are quite
as aged . . . . It is more probably an innate
conservatism; a conservatism founded
genetically upon the fact that these irises
are descendants of a small and highly
selected stock."

Finally, it should be noted that recent
work by Wynne-Edwards ('37, '39) has

indicated considerable doubt that the
nunatak hypothesis, which is coupled with
the concept of species senescence, is
everywhere valid as an explanation of
the local occurrence of the epibiotics.
Wynne-Edwards ('37) has shown that
great numbers of the Cordilleran species
in the east are restricted to the local areas
of soils derived from basic rocks. Fur-
thermore, the rate of rock exfoliation in
proximity to continental ice sheets is so
rapid in many rocks as to obliterate all
traces of glaciation within a length of
time much less than the post-Wisconsin
(Wynne-Edwards, '39). Thus it is pos-
sible that many of the so-called nunataks
were glaciated.

There would seem to be no need for
the concept of species senescence. It is
replaced by the idea of populations of nar-
row ecological amplitude because of ge-
netic reasons. Their simpler genetic con-
stitution results from their vegetational
history. Their restricted and scattered
occurrences result from the restricted and
scattered occurrences of habitats which
are suitable for such species.

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# DETERIORATION OF MIDWESTERN RANGES [*][1]

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The native grasses of the mixed prairie and short-grass plains disclimax have been subjected for a long period of years to extreme drought, much overstocking, and severe damage from dust. Behavior of the vegetation during the dry 'year of 1933, the extreme drought of 1934, and the terrible dust storms and intermittent periods of desiccation during subsequent years, has been continuously observed (Weaver and Albertson, '36). Previous studies in this area furnished a background which enabled one to compare present conditions with those of the pre-drought period (Weaver, '24; Clements and Weaver, '24; Albertson, '37). A large series of exclosures and permanent quadrats supplemented by phytometers and measurements of environmental factors have revealed the nature and causes of changes in vegetation over extensive areas in western Kansas. While these data are being evaluated, and especially because of the recurrent severity of the summer drought of the present year (1939), it seemed advisable to compare the grasslands of the western half of Kansas with those of a much wider area which has undergone similar vicissitudes.

During August, a careful study was made of pastures and range lands of western Kansas and Nebraska and portions of South Dakota, and of great areas in eastern Wyoming and Colorado, and the Panhandle of Oklahoma. Eighty-eight representative ranges have been examined in the six states, including several that have been under observation for a period of ten or more years.

This survey of the midwestern grasslands (exclusive of vegetation on light, sandy soils) consisted very largely in a study of two great dominants which are, with exceptions, the most important and often nearly the sole components of the vegetation. These are blue grama grass, *Bouteloua gracilis*, and buffalo grass, *Buchloe dactyloides*. *Carex stenophylla* and *C. filifolia* (niggerwool) were important in certain areas northward; needle-and-thread, *Stipa comata*, and western wheat grass, *Agropyron smithii*, also were often intermixed with the short grasses, especially in the more northerly ranges. But the sod-formers and not the bunch grasses have become relatively more abundant since the advent of overgrazing, and the latter have also suffered far greater losses during the drought. One of the most outstanding effects of drought upon the grasses is the usually uniform distribution of the remaining individuals.

## THINNING OF THE PLANT POPULATION

When the great drought came, it alone rarely or never killed all of the vegetation. The effect was that of thinning the stand. In this selective process many of the less xeric species of grasses and forbs were killed outright and today only a few dwarfed relicts are to be found, often after long search in the most favorable situations. Among the most drought resistant grasses, it seems certain that the younger and consequently more poorly rooted individuals succumbed. Likewise, the less vigorous among the older and long established plants were destroyed. Much of this thinning occurred as a result of the intense heat and extended drought of 1934, but losses continued in 1936 and 1937 and recurred at other times during the seven-year period of general desiccation. The normal precipitation of 17 inches over the western edge of the
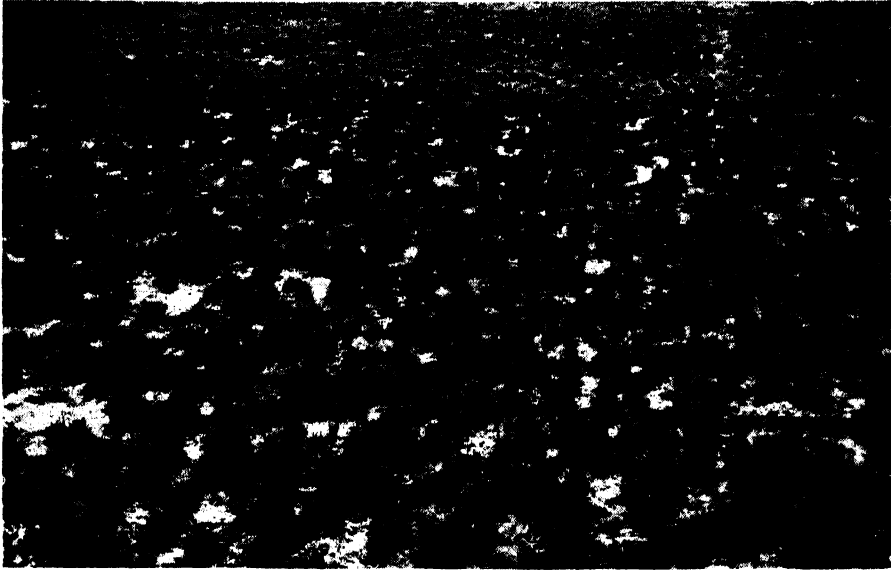
FIG. 1. A formerly fine range of blue grama and buffalo grass on hard land near Seibert, Colo., illustrative of the better pasture conditions today. The basal cover of about 85 per cent is now reduced to 18. Note the wide spacing of the individuals and the fact that all portions of the range have some grass remnants. The buffalo grass occurs in small bunches or rows and constitutes about one-third of the vegetation.

region often fell as low as 6 inches. Amount of destruction and the extreme test experienced by the survivors may be understood when it is known that many excellent ranges with 65 to 90 per cent basal cover have been reduced usually to a scant cover ranging between 20 and 1 per cent (figs. 1, 2, and 3).

Death among the perennial forb population was so widespread during the initial severe period or similar recurring ones that today only scattered individuals of six or eight species regularly occur. By practically eliminating species least fitted to endure hardships and by wide spacing of those best adapted, the grassland has adjusted itself to the new environment imposed upon it. Even widely spaced survivors have barely the necessary amount of soil moisture for their existence. Such an ecological process parallels in a general way that of the human population. Extensive abandonment of ranches and emigrations of settlers have been followed by wider spacings and larger holdings of the remaining population, most of whom have learned by long experience how to endure the hardships of drought.

CAUSES OF DAMAGE TO THE RANGE

Although the ranges have been depleted in stand, vigor, and carrying capacity as a result of the great drought, damage has not been due to intense heat and desiccation alone. Overgrazing and untimely pasturing of many ranges before this great catastrophe subjected them to the onslaught of desiccation in a much weakened condition. Moreover, during this long period of adversity much pasture land has literally been stripped of the last vestige of vegetation by hungry stock and grasshoppers. Despite these adversities, extensive areas throughout the range country would have survived with only moderate losses had it not been for partial or complete burial by dust, or for injury by wind erosion and attending disastrous consequences. Damage to grassland has been enormously increased as a consequence of injudicious breaking and unwise tilling of enormous stretches

of range lands. As stated by Newport ('37) for the southwestern Great Plains:

Recent years of agricultural expansion destroyed vast areas of native sod. The depression which followed, coupled with severe droughts, frequently resulted in indifferent farming or outright abandonment. The bare, unprotected soil was readily moved by the preying winds. Overgrazing joined with drought and was aided in the erosional process by the abandonment of neighboring fields. Depletion of land, often complete denudation was the result.
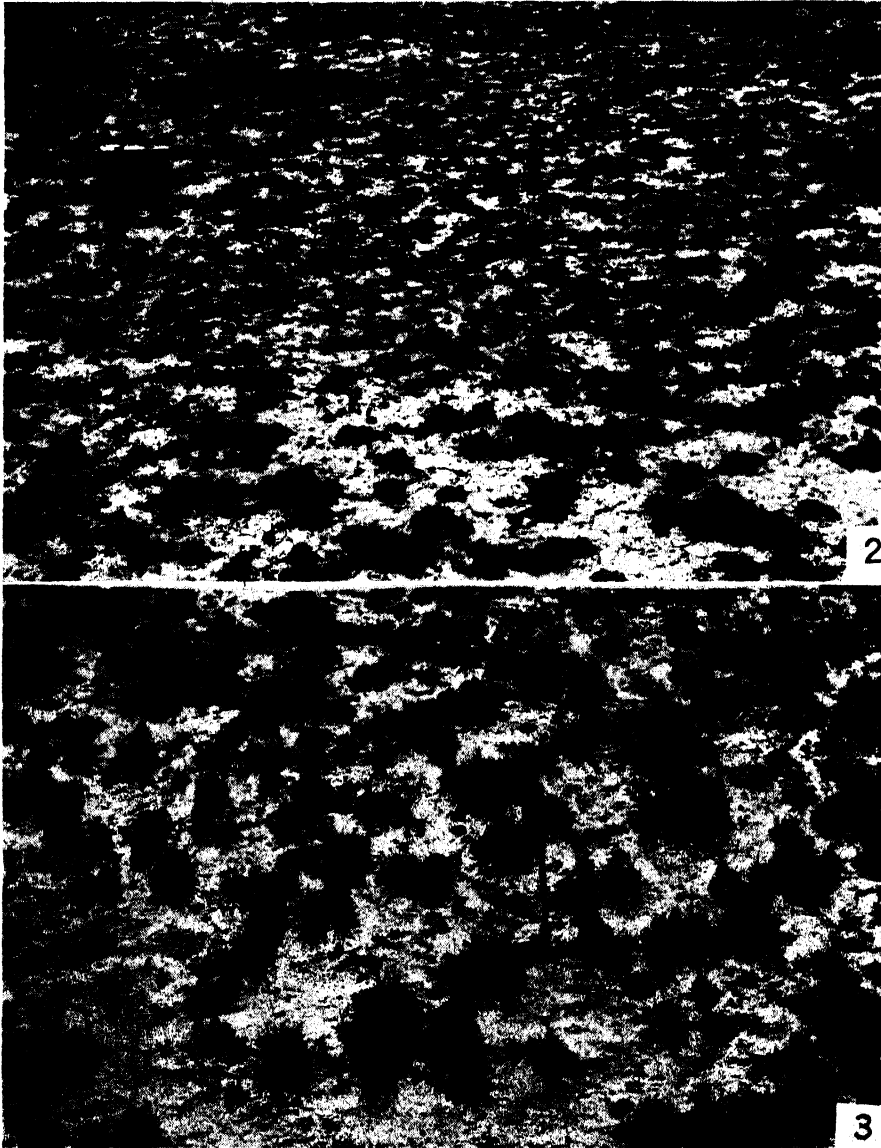


Fig. 2. Pasture on hard land near Brush, Colo. The former basal cover of 70 to 80 per cent has been reduced to about 8 per cent. Of this, however, approximately only 1 per cent remains alive. Practically the entire cover is blue grama grass.

Fig. 3. Sample area of grama-buffalo grass range near Eads, Colo., which has been very much overgrazed and trampled. This is representative of the entire large level pasture with a former cover of 80 to 85 per cent, but now reduced to 2 per cent in many places. Note the dead crowns of the grasses to the left of the pencil. Large, entirely bare areas, however, did not occur.

## OVERSTOCKING AND UNDERSTOCKING

A survey of the situation reveals clearly that too close grazing of the buffalo-grama grass ranges usually occurred where stock raising was carried on in conjunction with production of farm crops. Too much grazing pressure was permitted in pastures of moderate size (80 to 160 acres or more). This occurred somewhat regularly both before and often during the drought. Overgrazing even of the extremely resistant short grasses is doubly harmful. Not only is the vigor of the tops and crowns greatly reduced
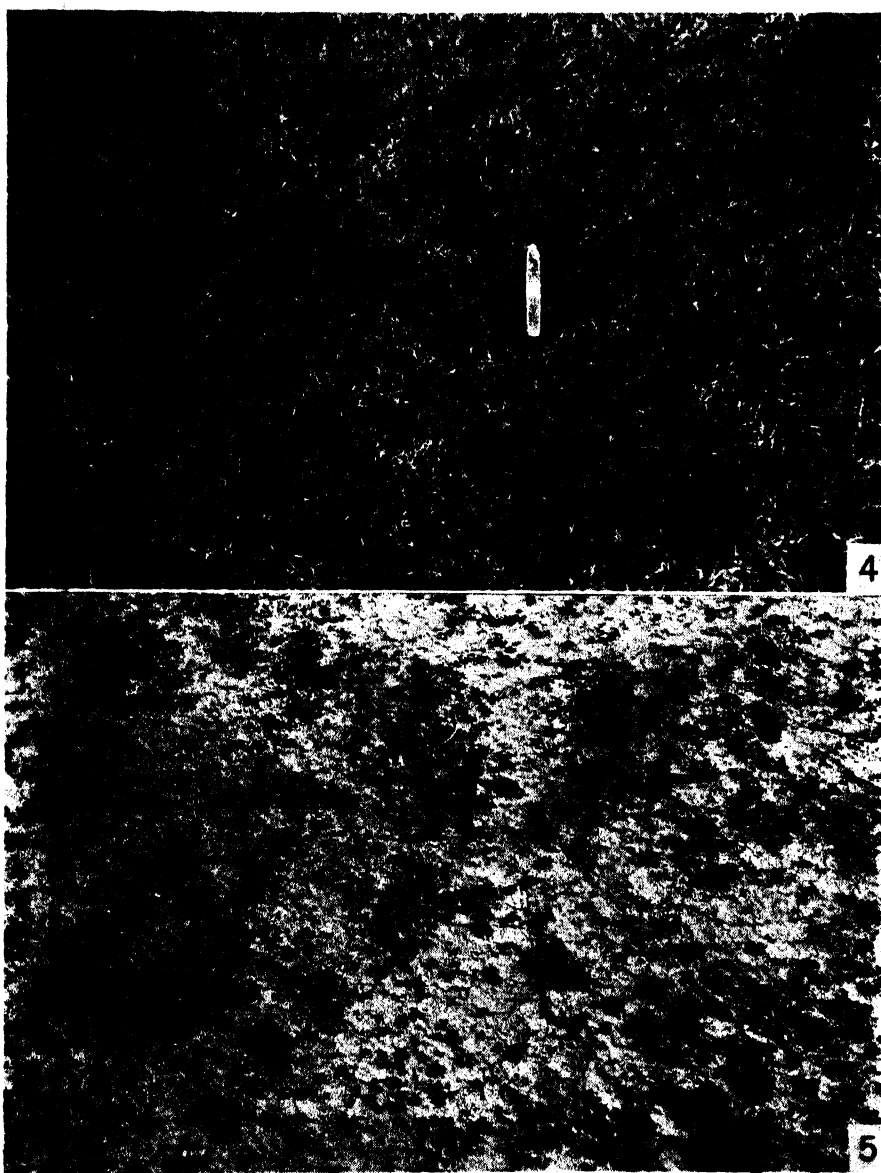


FIG. 4. Detail of vegetation in a pasture of 160 acres near Scott City, Kans., in 1937. Despite the previous drought damage, this buffalo-grama grass range is in good condition with a cover well reestablished since the 1934 drought, although it is now being grazed to within an inch of the soil.

FIG. 5. Detail of the same pasture in 1939. Owing to excessive grazing and trampling scarcely a living plant remains, though the dead crowns bear mute evidence of its previous condition as shown in figure 4.

and the store of reserve food therein constantly decreased, but also the root system itself is greatly weakened by reduction in depth, lateral spread, and in efficiency as an absorbing organ. Any slight gains by stolon production may be immediately checked (figs. 4 and 5). On larger holdings, pastures are many square miles in area; not infrequently, the sweep of unbroken, level or undulating range land extends to the horizon on all sides. Where stock raising is the chief industry, usually more attention has been given to grazing practice on these privately owned ranges. But even here the pressure of starving stock during the early drought resulted in a high degree of overgrazing, and subsequent adverse conditions have prevented much recovery even where cattle have been shipped out. Nearly all
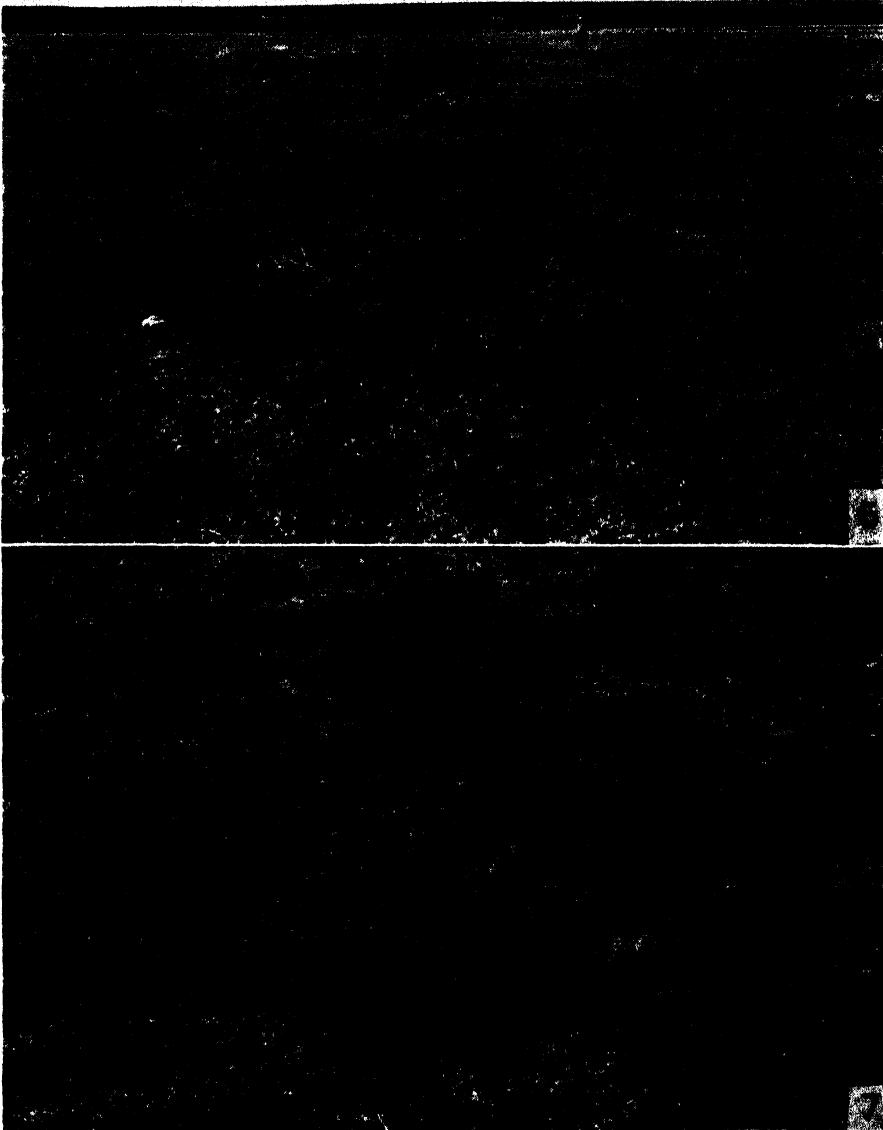


FIG. 6. Low lying land in the valley of Ladder Creek near Tribune, Kans., where protection from dust, moisture from run-in water, and judicious grazing maintained an excellent stand of short grasses.

FIG. 7. Detail of typical complete cover of buffalo-grama grass range shown in figure 6.

of the ranges observed had been exces-
sively grazed.

In the midst of range lands greatly
depleted by drought and dust damage,
however, one finds favorably located tracts
of land where damage to the range, if
any, must be attributed largely to grazing
abuses alone.   A striking example is a
low-lying, almost level area north of Trib-
une, Kansas.   It is several square miles



FIG. 8.   Overgrazed area in same valley across the fence from the preceding.
The cover is reduced to about 20 per cent, *Lappula occidentalis, Monolepis nuttal-
liana*, and other annual weeds are abundant, and much bare soil is exposed.

FIG. 9.   Short-grass pasture near Alma, Nebr., showing abundance of buffalo
grass (light colored) and blue grama grass (in bloom in front of black cloth).
This is a good pasture, conservatively used and weeds are practically absent.
While patches of sand dropseed (*Sporobolus cryptandrus*) occur in the broken
sod (see foreground), they are relatively small except on the hills where cattle
trample and graze closely (Photo. August 15, 1939).

in extent and nearly surrounded by grass-covered hills, the unbroken range extending well back over the upland. Consequently, there was no deposit of dust on the excellent growth of buffalo and grama grass sod which was favored by run-in water from the slopes. The basal cover was 95 per cent and the foliage almost completely concealed the soil (figs. 6 and 7). This, of course, was the result of good range management and decreased grazing pressure during the dry years. But portions of this lowland had suffered from overstocking. This was shown by the common occurrence and spread of cacti, by reduction of the basal cover (which was scarcely exceeded by the foliage cover) to 20 per cent, and by the presence of an abundance of weedy annuals (fig. 8).

Exceptions to general range damage by whatever cause sometimes occur. These may be due to opportune rains having permitted a previous return toward normal, to more judicious range management, or to protection from damage by dust burial.

During the extreme periods of drought

of the past 7 years, it has been necessary intermittently to ship starving cattle to eastern and southern pastures. In many instances, notably in central and western Kansas and Nebraska, the herds have not been replaced (or only in part) and pastures are undergoing year-long protection or, at least, light grazing. Many such ranges have somewhat recovered from drought depletion. In the eastern portion of the region with mean annual precipitation of 20 to 23 inches, increase in abundance and vigor of the vegetation is often marked. Buffalo grass, especially, has reclaimed much formerly bare area by means of rapidly spreading stolons, and mats of this grass, frequently 4 to 6 inches thick, completely conceal the soil. In the drier ranges farther westward, recovery has often been very slow even under protection, so greatly were the plants weakened and so limited has been the precipitation (figs. 9 and 10).

NATURE OF INJURY FROM DUST

Accompanying the extremely high temperatures and almost rainless summers
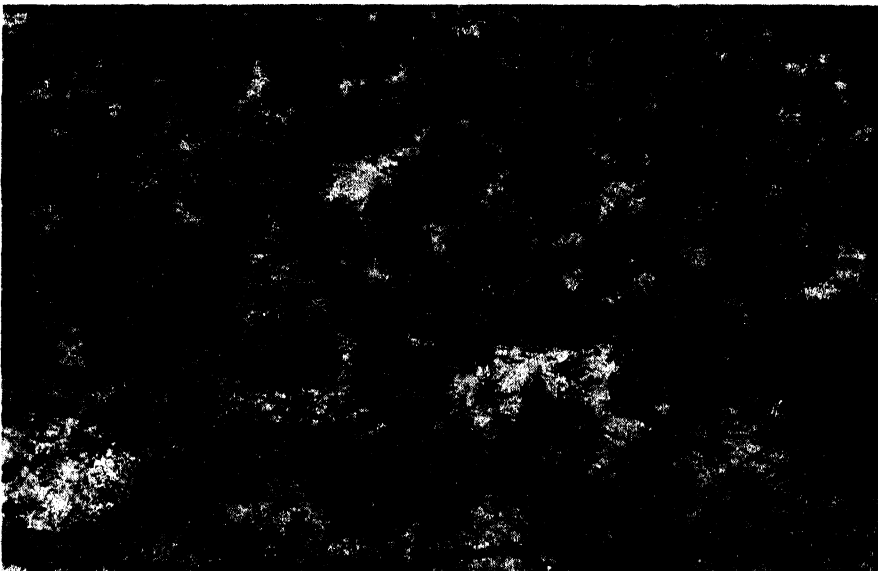


FIG. 10. Detail of buffalo-grama grass range on hard land near Springfield, Colo. The basal cover averaged about 40 per cent and the plants are vigorous. With continued decrease in grazing pressure and moderately favorable rainfall, this network of vegetation will soon reestablish the original nearly complete cover.
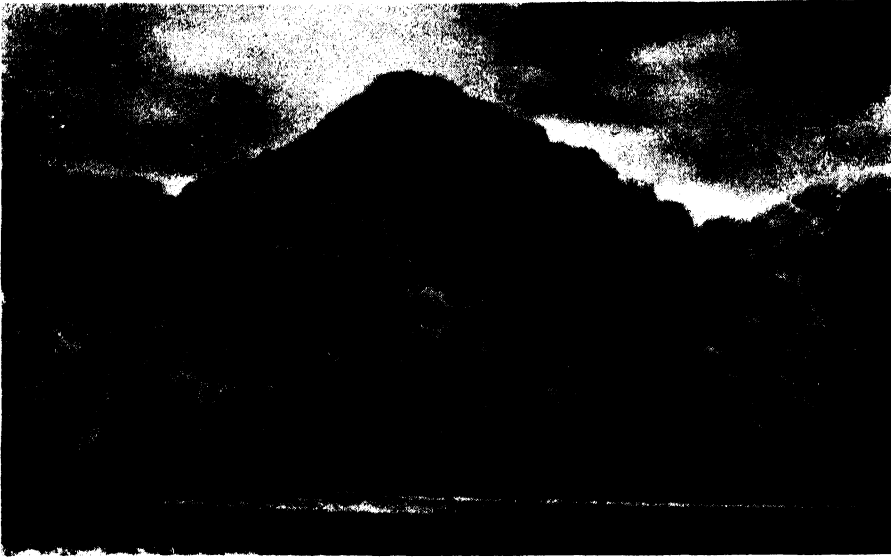
FIG. 11. Approaching dust storm in the middle west. Photo. by Conard.

were unusually high winds. These great storms carried enormous amounts of earth from parched fallow fields and cropped land and deposited it on other fields and pastures (fig. 11). The depth of deposit varied greatly depending upon distance from the source of supply, topography, and nature of vegetation. Whether a good cover of native vegetation or a depleted, weedy one offered obstruction to the dust laden wind, the result was a covering of soil more or less uniformly deposited to a depth of .5 to 2 or more inches. Dust drifts and mounds sometimes to 2 to 3 feet or more in height were formed. Often the grasses were only partially destroyed, but in many instances practically all vegetation was smothered. It should be emphasized, that had the land not been broken, decrease in the amount of vegetation would have certainly resulted from the intense heat and drought, but not such overwhelming denudation. An enormous amount of dusting, as this phenomenon is designated in the affected region, occurred in the spring of 1935. Even when the compacted dust deposit reached a depth of only an inch, it usually killed much of the short-grass cover.

After the dust-covered vegetation died

and disintegrated, the tops no longer held the soil against wind erosion. Once more the soil began to shift before the force of the wind. Much of it was transported, often to be deposited in drifts 1.5 to 2 feet or more high where centers of accumulation were afforded by the crop of annuals, most generally Russian thistles, which had previously sprung up in the pastures. Much drifting in pastures occurred in 1937 and 1938, when great areas of grassland were laid bare by the blowing away of the accumulated silt. Indeed, the chief source of supply of silt for some of the worst dust storms during these years was from the earth formerly deposited in pastures.

Abundant evidence of the sequence of deposit and subsequent erosion—sometimes by torrential rains as well as by wind—was offered by the dead crowns and decaying stolons of the grasses, which usually remained plainly in view on the windswept, bare surface. The roots were still anchoring them in place. Other evidence was found in the crowns and taproots of forbs, a few of which often remained alive as much dwarfed survivors. In many instances two or three years elapsed before the former soil surface was uncovered.
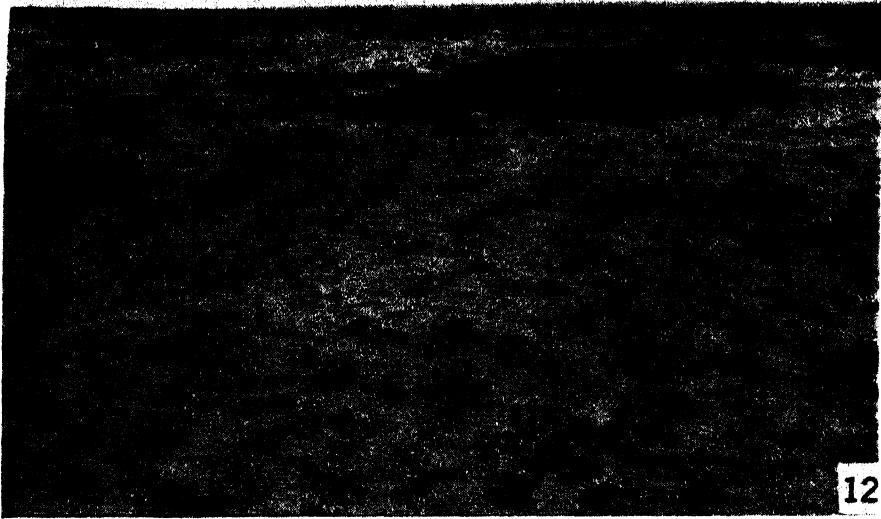
FIG. 12. Former buffalo-grama grass range on hard land near Lamar, Colo. A very extensive area has been covered with dust which has smothered the vegetation. Upon the death of the plants, the wind has blown the soil clean in places and heaped it up into irregular mounds 3 to 15 feet long to a height of 1 to 2.5 feet wherever Russian thistle or other obstacle furnished a nucleus for deposit. The dead crowns of buffalo and grama grass, the latter sometimes grouped in sods 6 inches in diameter, are now 3 to 6 inches above the general soil level. Figures 1 and 3 also show elevation resulting from water and wind erosion.

FIG. 13. Portion of a large, level, dust-covered pasture near Limon, Colo. The cover (bunches) of blue grama and buffalo grass has been decreased to less than one per cent. These widely spaced clumps are not only alive but have increased in size subsequent to their partial burial. Only a few of the most drought resisting perennial forbs have survived. Many annuals have made a precarious growth, succumbed to drought, and given the landscape its gray, barren aspect.
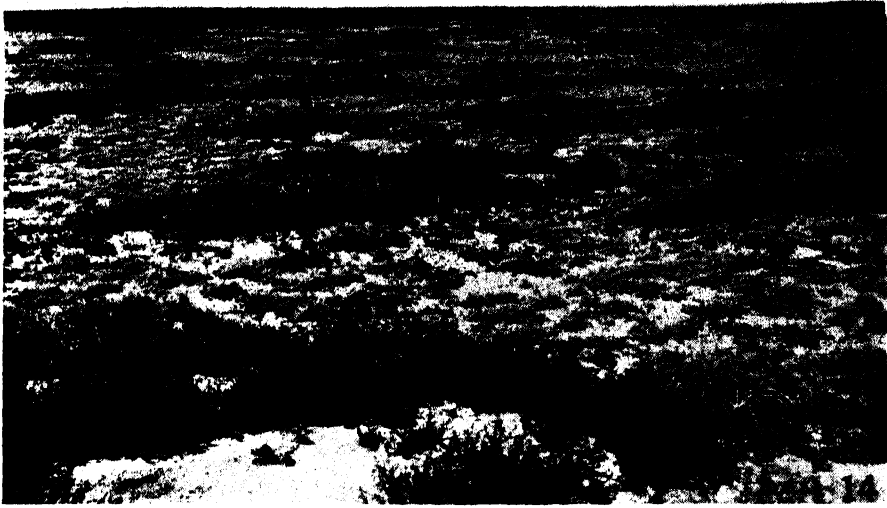
Fig. 14. Portion of a quarter section of range land near Springfield, Colo., farthest from cultivated fields and consequently least damaged by dust. Fully nine-tenths of this pasture was buried so deeply that practically all of the grasses were killed and the dead crowns again exposed. It is now a waste of Russian thistles. In the best portion, the areas between the heaps of silt, which support thistles, have a surviving cover of 18 to 20 per cent.

The scarifying action of dust-laden winds contributed to the death of many pasture plants. Smaller pastures of 80 to 160 acres in area were often wholly surrounded by cultivated fields. They suffered more injury than larger ones. Partial dust burial often caused the living vegetation to reestablish its base 1 to 4 inches above the former soil level. Thus, when the loose soil was later removed, or when erosion lowered the old soil level, the plants, including various forbs, were elevated on columns quite above the surrounding soil. This exposure, of course, aggravated drought and most of the plants died (fig. 12).

Pastures were sometimes listed in order to check the removal of blowing soil. This usually held the soil on the field and promoted an excellent growth of annual weeds but practically destroyed the native plants. So thoroughly did the soil deposits from fields and the subsequent drifting destroy the vegetation, that after the roots and rhizomes decayed, wheat was drilled on the one-time range without further preparation of a seedbed.

Some of the greatest losses to ranges by dust burial probably occurred in and adjacent to the Panhandle of Oklahoma, which with considerable areas in the four adjoining states is designated as the dust bowl. This resulted from a combination of factors, one of which was the large amount of tilled land that furnished an unlimited amount of wind-blown soil. But similar damage was found throughout western Kansas and Nebraska, and in Wyoming, as well as throughout eastern Colorado. It is a very general rather than a local phenomenon and is apt to recur wherever unprotected, drought-parched soil adjacent to grassland is subjected to high winds (figs. 13 and 14).

## DAMAGE BY GRASSHOPPERS

Still another factor in reducing the vigor of vegetation was the hordes of grasshoppers which accompanied the drought. For example, from 8 to 15 per square foot were observed during the summer on certain ranges in western Kansas. They ate the leaves and tender stems of the grasses, stripped the foliage

of the ubiquitous peppergrass and Russian thistle, and devoured nearly all vegetation including the only plant cover remaining in many pastures—the mat-like *Monolepis nuttalliana*. Even on ranges where stock was excluded, grasshoppers had sometimes eaten practically all of the scanty growth of vegetation. Moreover, buffalo grass was particularly retarded in its development not only by the injury or loss of foliage, but the always hungry grasshoppers cut the stolons at the nodes where they are tender and where the growing tissue is sweet. Thus segregated from the parent plant, the poorly rooted, younger offspring succumbed.

## CHANGES IN STRUCTURE OF VEGETATION

As a result of the combined forces causing deterioration in range and pasture, there have been marked changes in vegetational structure. The mixed prairie, distinguished by more or less distinct layers of mid grasses and short grasses, has, at least in the several thousand square miles examined, almost entirely been converted into short-grass plains. This has resulted from the loss of the mid grasses. Before the great drought, it is true, there were many ranges that had lost most of the vegetation of the upper layer through continuous overgrazing. But relicts were always present and usually abundant in wet years. Moreover, adjacent grassland less severely abused showed clearly the true nature of this relationship. This grazing disclimax is much more pronounced today, and extends quite to the eastern border of the association. Since 1932, the writers have recorded from year to year the increasing losses of *Andropogon scoparius, Aristida longiseta, A. purpurea, Sitanion hystrix,* and other mid-grasses and accompanying forbs. Today an open short-grass carpet with widely spaced, most xeric forbs alone remains. This conversion of mixed prairie to a short-grass disclimax is indeed one of the most interesting features of this grassland.

Over vast stretches, in 1939, the sev-

eral species of *Aristida, Sitanion hystrix, Koeleria cristata, Stipa comata, Andropogon scoparius,* and *Agropyron smithii* were entirely absent. Undoubtedly remnants remain underground and in favored places, but the long-time drought and the grazing of the grass almost into the soil have been extremely destructive to the mid grasses.

Many of the less xeric forbs such as *Astragalus crassicarpus, A. mollissimus, Lepachys columnaris, Antennaria campestris, Grindelia squarrosa,* and others have likewise practically vanished. Certain of the most persistent native forbs were nearly always present in this survey, often as mere remnants. The most drought resistant are *Malvastrum coccineum, Sideranthus spinulosus, Lygodesmia juncea,* and *Allionia linearis. Psoralea tenuiflora, Liatris punctata,* and *Cirsium undulatum* are slightly less so. *Kuhnia glutinosa* and (southwestward) *K. hitchcockii* are likewise very resistant to drought injury. Even these xeric forbs were always greatly dwarfed and usually only 2 to 5 inches tall. Early spring revealed an abundance of *Anemone caroliniana* and *Allium nuttallii,* plants with large storage organs, but these soon disappeared above ground.

The opening up of the plant cover and the abundance of bare soil permitted the growth of hordes of short-lived annuals, some of which were so thickly placed as to quite obscure the remaining grasses. Among the most persistent and widely distributed were *Lepidium densiflorum, Lappula occidentalis, Hordeum pusillum, Plantago purshii, P. spinulosa, Monolepis nuttalliana,* and *Cryptantha crassisepala.* But they were soon overtaken by drought, their dead remains giving the dull leaden gray or, later, black color to the landscape.

Sometimes the pastures were reddened after a period of showers by a thick growth of *Portulaca oleracea.* More frequently they varied through several shades of green, depending upon the direction of the incident light, and finally to black as the ubiquitous Russian thistles pro-
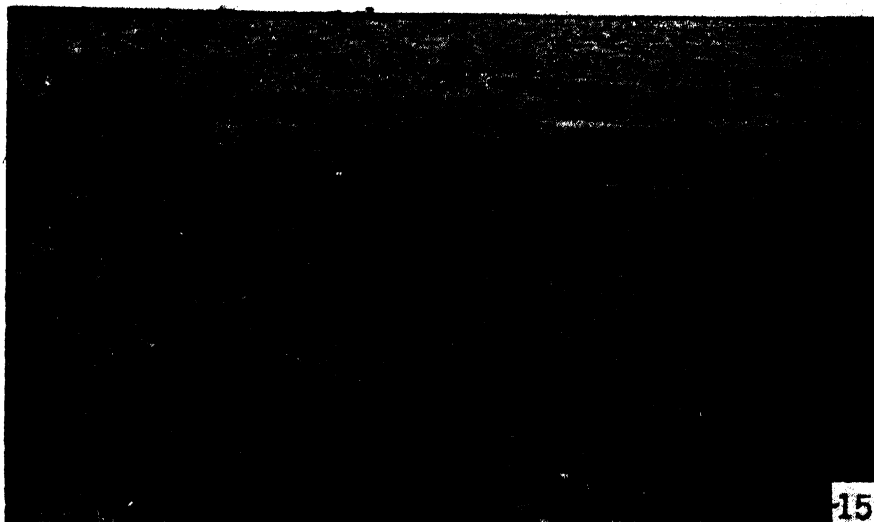
FIG. 15. Pasture of blue grama grass near Carpenter in southern Wyoming, where about one-fifth of the area is occupied by cactus. The grass cover averages 20 per cent but only a few live shoots were present in the many bunches examined. The cacti are elevated somewhat on accumulated dust heaps. All but the cactus was grazed by sheep to within one-half inch of the soil. *Malvastrum coccineum, Sideranthus spinulosus, Liatris punctata*, and *Psoralea tenuiflora* were the only other living perennials.



FIG. 16. Range of blue grama and niggerwool with traces of sand dropseed, wheat grass, etc., near the South Dakota-Wyoming state line west of Custer. Cactus occupies about 20 per cent of the area and the closely grazed grasses furnish a 20 per cent cover over the remainder.

FIG. 17. Propagation of cactus by seedlings. The youngest, about 3 months old, is near the pencil; those with a single flat joint are probably one year old, while the plant showing 8 branches (beyond the pencil) has grown for several seasons. Note the typical openness of the vegetation in the foreground. Photo. August 18, 1939, near Limon, Colo.

ceeded through their early stages of development until they were killed and dried by drought. Large numbers of annuals—notably *Amaranthus retroflexus, A. blitoides, A. graecizans, Chenopodium album, C. leptophyllum,* and *Solanum rostratum*—were scattered in dusted pastures or grew thickly in the deposits of silt. Their stature was determined by the rainfall; they were mostly dwarfed in 1939 and only infrequently exceeded a height of 2 to 6 inches.

One of the worst perennial weeds is the cactus. Several genera are concerned but by far the most important are the species of *Opuntia*. The increase in numbers has resulted from the opening up of the grass cover. Even before the great drought many ranges were highly infested as a result of too close grazing. Since the great destruction wrought by this recent disaster, cactus has increased almost throughout. Much branched, circular individuals 3 to 5 feet or more in diameter and spaced only 6 to 10 feet apart occupy a large portion of the range land (figs. 15 and 16). Occupancy of

20 per cent of the soil by this pest is not uncommon. Ranges with greatly increased numbers and with only 50 to 25 per cent of the soil unoccupied by cacti occur. Some ranges are thus entirely worthless for grazing, and even jack rabbits are said to avoid them. Propagation in bare soil is rapid; it has been estimated that these plants are now 4 to 7 times as abundant as in 1934. Seedlings occur in untold millions, and are especially abundant about the parent plants. Joints of the stems are broken off by stock and frequently become rooted when the surface soil is moist, thus increasing the number (fig. 17).

In eradication of cactus by scraping them from the soil with a grader blade and removing them from the range, it is necessary to repeat the operation when the millions of shoots again grow from the fleshy crowns and roots. Manyspine prickly pear, *Opuntia polyacantha,* is very difficult to eradicate by grubbing because its widely spreading underground parts are capable of producing many new shoots (Harvey, '36). Although many

cacti were weakened by long periods of wilting, so intense and prolonged was the drought, yet it is probable that few died directly as a result of the heat and lack of water. They remained on areas of level land which were eroded as bare as a floor, except for the cacti, by dust laden wind. Burial by drifts of dust was fatal to many or to all in various situations, as is shown by their dead remains after the
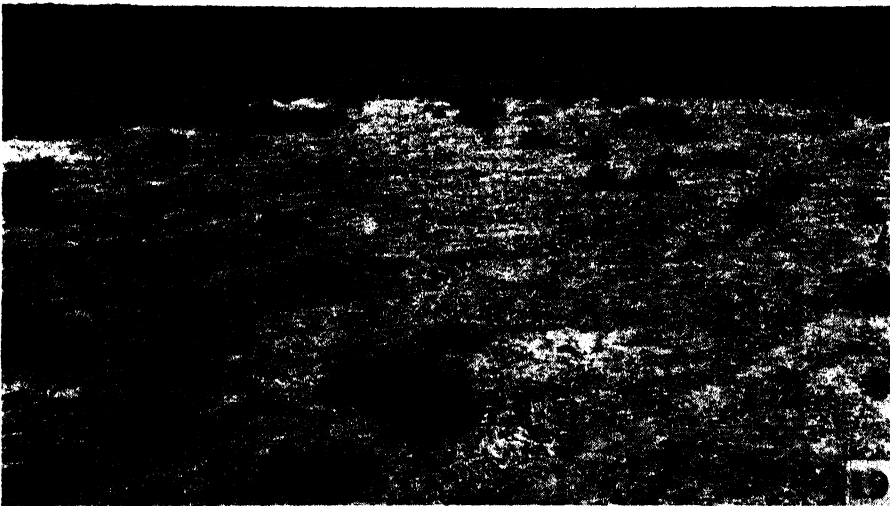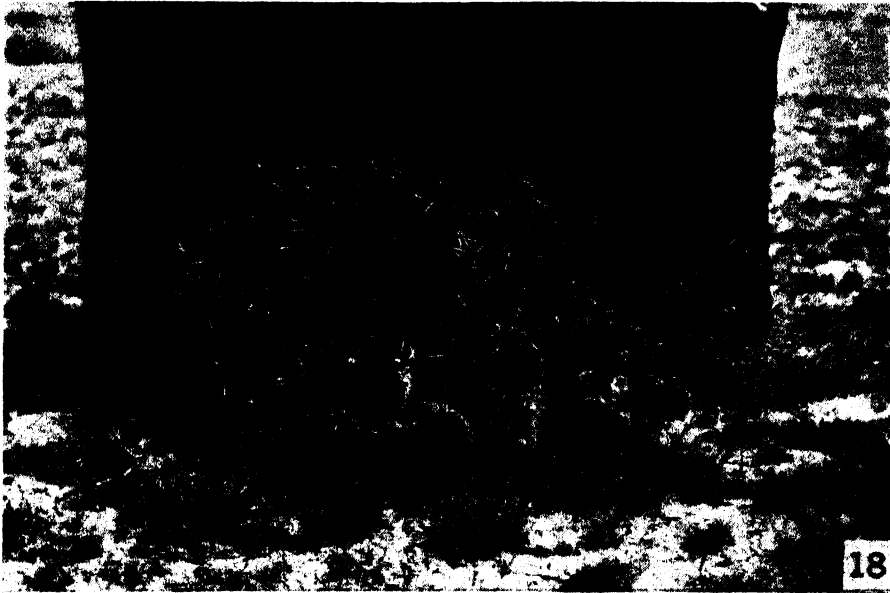




Fig. 18. Blue grama producing seed in a closely grazed range near Limon, Colo. Several of these bases often occur in a square rod. Where the cacti are smaller and isolated, grasses are less abundant and shorter. The surrounding vegetation, mostly blue grama, furnished a basal cover of only 15 per cent. The former vegetation was approximately one-half buffalo grass. Buffalo grass seems less drought resistant and sometimes almost completely disappears.

Fig. 19. Pasture near Oakley, Kans. The whole area has been dust-covered and the dust later removed. Russian thistles occur in the foreground and a dense, continuous growth of peppergrass 3 to 6 inches tall clothes the background. All grasses have been killed.

dust was again blown away. Elsewhere they grew upward through the accumulating heaps of silt and are now commonly elevated 4 to 6 inches above the former soil level. Other destructive agents are caterpillars, grubs, cochineal bugs, etc. Unless eradicated by man, however, many decades must probably elapse under the most favorable climatic conditions before the recuperated grasses can reclaim this territory once held by them.

Cacti, however, like most weeds, render certain valuable services in nature. Such are stabilizing the soil against wind and running water and furnishing oases of protection for range grasses against grazing animals (fig. 18). Here many species reproduce unharmed. Snow accumulates, and runoff water is dammed back until it enters the soil. The seedling grasses and forbs grow in partial shade and evaporation from the soil surface is much reduced. Where the cactus plants merge, such havens may extend several yards, often at right angles to the slope, and thus afford considerable areas for seed production by grasses and forbs. Buffalo grass is less likely to thrive, because of its unfavorable reaction to shade and the accumulated debris.

### Pasture or Field

So great has been the disturbance to the grassland and so regularly have ruderals taken possession that it is frequently difficult to determine, except by close study, whether or not the land has been tilled. The landscape in summer for miles about is often one of Russian thistles in field and pasture (figs. 19, 20, and 21).

Reconstruction of the original cover from the dead remains is an interesting task. The fragments of rootstocks, the bits of stolons, the strong taproots of forbs, and even the grass roots themselves, together with comparison of adjacent more protected areas, make identification certain. Whether the dusting is recent or occurred during the earlier

years of drought can often be determined. Previous knowledge of the area when vegetation was intact, and study during the several processes of deposit and denudation, as has been the opportunity of the writers, lends certainty to the exactness of sequence.

### Degree of Deterioration

Drought damage to grasslands in true prairie can readily be determined, since many areas of variable size, often 80 to 160 acres or more, are kept for the production of hay, and stock is excluded (Weaver, Stoddart, and Noll, '35; Weaver and Albertson, '36 and '39). This, however, is not the practice in the mixed prairie, except on the extreme eastern edge, and on low lands unusually favored by run-in water. Practically all grassland is grazed, at least during drought. Hence, the present study is one of pastures and ranges.

A total of 88 well spaced, typical areas on non-sandy lands in the six states were carefully examined and basal cover determined. According to the amount of remaining cover of range grasses, they have been separated into five groups. Ranges with a cover of 21 per cent or more (exclusive of weeds) formed only 16 per cent of the total. Those with 11 to 20 per cent cover constituted another 16 per cent. The largest group, 28 per cent, presented a cover of 6 to 10 per cent. The basal cover of another 16 per cent ranged from 2 to 5 per cent, while nearly one-fourth of the grasslands (24 per cent) had a basal cover of only 1 per cent or less. Distribution of the good and bad conditions were not at all uniform. This was to be expected when so many causes or combinations of causes have operated to produce degeneration. The outstanding fact is the very poor cover.

### Further Depletion or Recovery

Long continued drought imposes ever increasing hardships upon an already

weakened plant population. Drought has now prevailed, although intermittently, for a period of seven years. At the beginning of the catastrophe the store of seed on and in the soil was great. With the advent of showers many of the seeds germinated and developed seedlings, only to be destroyed by lack of a further moisture supply. This process has been repeated again and again, each interval of relief from drought witnessing the appearance of successively fewer seedlings,
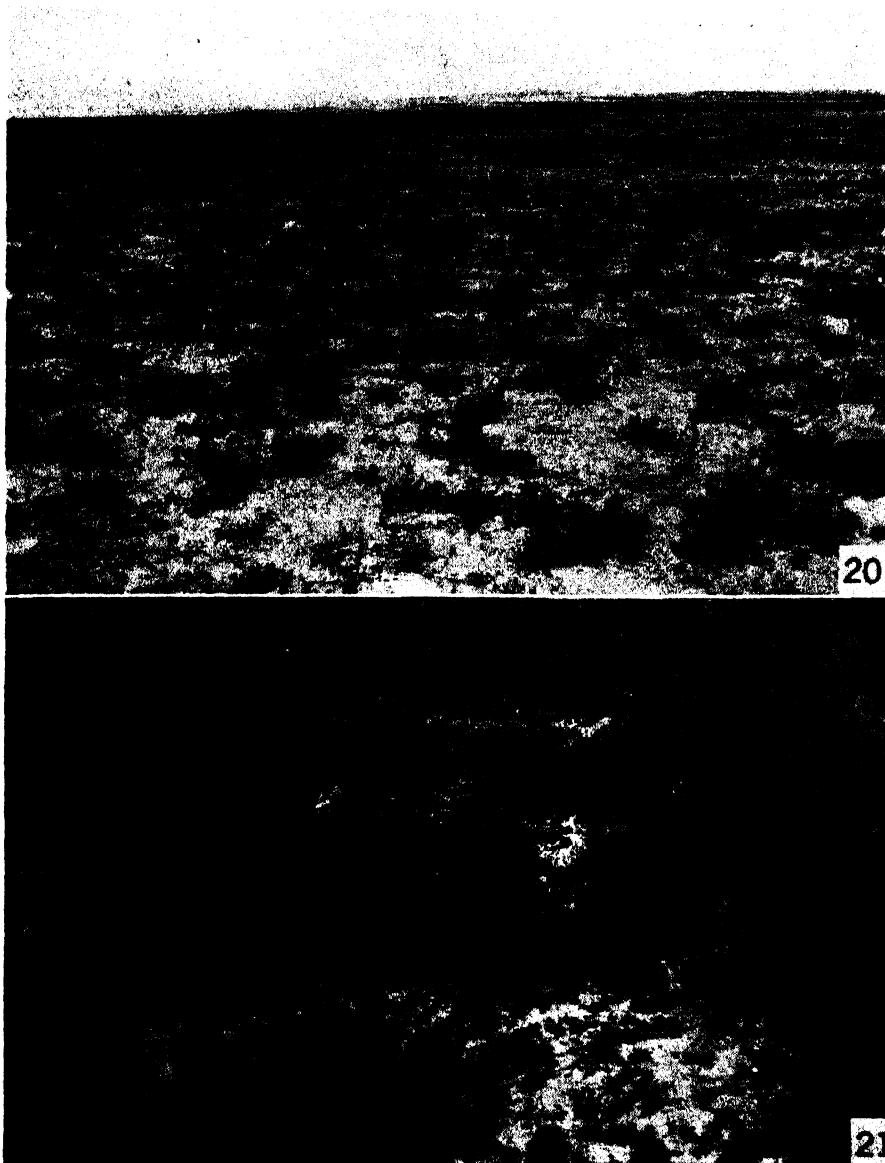


FIG. 20. Appearance of range near the Jay Em Ranch about 30 miles south of Lusk, Wyo. The soil is slightly sandy. The conspicuous plants are Russian thistles. The original cover consisted of blue grama, niggerwool, and needle grass, of which only remnants remain.

FIG. 21. Pasture near Boise City, Okla., on nearly level land that has been covered with silt and again uncovered. It is indistinguishable from the highway from weedy tilled land. Many of the Russian thistles are growing on drifts of soil. Although less than 1 per cent of the pasture cover remains, its former presence is clearly indicated by stolons and dead plant bases.

most of which met the same fate as the first. In addition, enormous supplies of seeds have been lost by dust burial, and by being eroded into low places and washed away. Thus the reserve may have been largely depleted. Moreover, fewer seed producing plants are available, and they are greatly weakened. Buffalo grass is not a good seeder normally, and blue grama tends to reseed
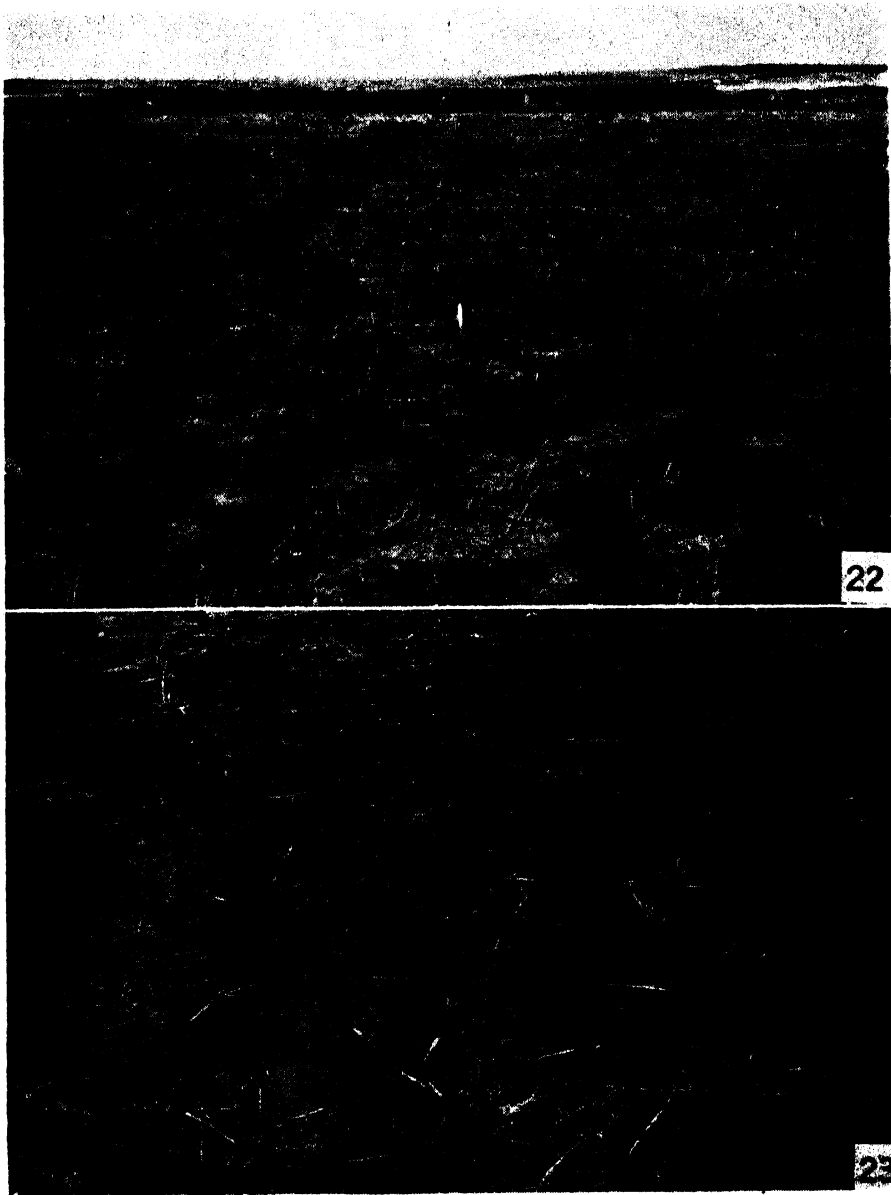


Fig. 22. A glimpse of an extensive overgrazed range near Ardmore, S. Dak. This is the blue grama-buffalo grass-wheat grass type. Although the dead stems of the mid grass are widely spaced, the rhizomes are alive and the tops would rapidly thicken up under protection and normal rainfall. The basal cover has been reduced to 10 per cent.

Fig. 23. Pasture near Lusk, Wyo., in needle grass-blue grama-niggerwool type, illustrating the evil effects of close grazing and trampling during drought. Basal cover is about 8 per cent. Grazing has been deferred until the stalks of the widely spaced bunches of Stipa were dry. They dried when only 6 inches long and have been trampled to the ground.

itself only slowly under conditions of grazing.

Conversely, many grass seeds are "hard" and remain viable for a very long time. In addition, various plains grasses, notably buffalo grass and blue grama can produce viable seed after only a few weeks of favorable weather for growth. Since scattered torrential rains occur over limited areas even during general severe drought, local new seed crops are usually produced each year. More-



FIG. 24. Windswept pasture near Meade, Kans., which was formerly covered with dust. The cacti are on mounds 6 to 12 inches high. There are still remnants of the short grasses although the cover, aside from cactus, is reduced to 5 per cent or less. In many parts of this large pasture, seedlings of sand dropseed and other grasses were scattered, often thickly.

FIG. 25. Range near Cimarron, Kans., seriously damaged by dust burial. Dead crowns show clearly that the previous cover was high, probably 80 per cent. Some seedling grasses were found but have scant protection, if any, from wind and sun. The chief weed is Russian thistle.

over, rhizomes of xeric grasses remain alive in the soil for many years, and from even scattered bunches of relict mid grasses reseeding occurs at a surprising rate during times of favorable moisture supply (figs. 22 and 23). In western

Kansas, for example, no grasses made any but slight growth during the spring and early summer of 1939. By midsummer they were completely dried. But responding to the rains of mid-August, flower stalks were produced in quantity
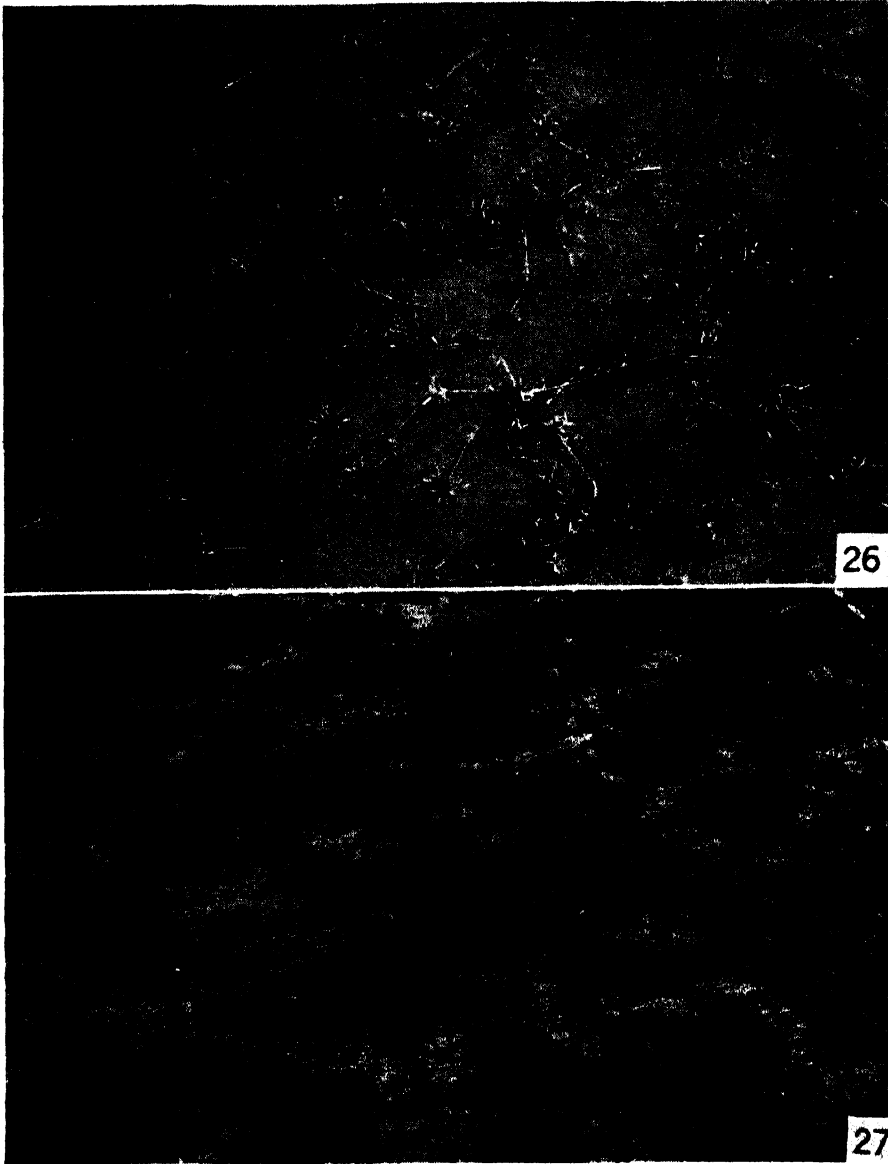


FIG. 26. Hard, windswept, level soil near Cimarron, Kans., where only a few widely spaced tufts of buffalo grass survived. Local showers permitted them to develop stolons, but the water supply was exhausted in mid summer and only the older and more deeply rooted offspring survived. This is typical of great areas where dusting has occurred.

FIG. 27. Buffalo grass pasture near Tyrone, Okla., showing the excellent recovery in almost pure stand, after great destruction as shown in figure 26. The proportions of grasses in this pasture are buffalo grass 85 per cent, blue grama 10, and sand dropseed about 5.

even from the widely spaced, drought relicts and some viable seed has been harvested. Such is the adaptation to life in the arid midwest.

Most pastures still contain sufficient grasses to provide a nucleus for rapid recovery under favorable climatic conditions (Savage, '37; Savage and Runyon, '37). Sand dropseed and side-oats grama, both prolific seeders, are widely scattered through this semiarid region. Many ranges, however, are so badly denuded that several favorable growing seasons will be required for them to develop a cover of good forage plants. The extremes approach abandoned, tilled fields where many believe 10 to 40 years is the necessary interval of time for the reestablishment of the climax (Clements and Chaney, '36).

Despite the arid summer of 1939, some pastures were found where surface moisture had been sufficient to promote the growth of abundant seedlings (figs. 24, 25, and 26). On bared areas, competition for water is less severe, unless weed infestations are very heavy, than in stabilized grassland. In fact, a moderate growth of taller cover is distinctly helpful in reseeding ranges. Abandoned lands are ordinarily prepared for grass seedlings by a previous crop of Sudan grass or other protective cover of an annual. This is mowed high to promote tillering but especially to prevent its forming seeds, later to develop seedlings which would compete with the young grasses for the precious water. The dead stubble and debris furnish protection from direct insolation, decrease evaporation, stabilize the soil by lessening the force of the wind in addition to increasing the supply of nutrients. A moderate growth of weeds in pastures and ranges has similar beneficial effects. If the tops of Russian thistles are mowed, the plants persist for a long time and do not so readily become detached from the soil and blow away (Savage, '39; Watson, '39).

During the period of drought certain mid grasses, notably side-oats grama and

sand dropseed, have increased enormously in the eastern border of mixed prairie. Of the two most common short grasses of this association, blue grama is the more drought resistant but the slowest to reclaim the territory of which it has been deprived. Its sole method of propagation, aside from the very slow one of tiller production and short rhizome-like stem bases, is by reseeding. Buffalo grass, when conditions are favorable to growth, spreads rapidly and widely. Hence many grama-buffalo grass ranges have been transformed into pastures of nearly pure buffalo grass (fig. 27). On the other hand, this species has often greatly decreased in proportion to grama grass, and in many pastures has almost entirely disappeared.

The drying and rejuvenation of short grasses are of regular occurrence even during normal years. In drought-dormancy the color assumed varies from that of freshly ripened straw to tan, and then to shades of brown. But in death the characteristic bluish-gray or dark drab color is revealed. In many of the ranges during late summer of 1939, the vegetation crackled like straw when tread upon or crunched like dry snow. By brushing even lightly with the hand, the shriveled tops could easily be crumbled away. Close inspection showed that a few green shoots spaced well apart remained imbedded in the dried crowns. These are the sparks of life that still remain despite the drought in some areas practically without effective rainfall for an entire growing season. But the dark colored, tinder dry, shriveled tufts in some pastures gave no such sign of life, in fact life seemed extinct. Much depends upon autumnal rainfall. Although the writers know well the almost incredible ability of these range grasses to regenerate after drought, yet it seems that soil moisture before winter is not only needed but is in many places imperative to survival. Without such rains even further increases in range deterioration are inevitable.

## SUMMARY

A survey was made in the summer of 1939 of 88 ranges selected as representative of grazing lands in western Kansas and Nebraska, portions of southwestern South Dakota, eastern Wyoming and Colorado, and the Panhandle of Oklahoma.

Severe drought, overgrazing, burial by dust, and damage by grasshoppers have resulted in greatly reducing the cover of range grasses.

This portion of the mixed prairie has almost completely lost its upper story of mid grasses on the non-sandy lands. The short grasses and sedges have undergone a process of thinning which has resulted in only the most vigorous plants remaining alive. Many of the less xeric forbs have practically disappeared and only six or eight of the most xeric native forbs are regularly represented by much dwarfed and widely spaced individuals.

The basal cover of grasses was 21 per cent or more in only 16 per cent of the ranges. In another 16 per cent it ranged between 11 and 20 per cent. It varied between 6 and 10 per cent in 28 per cent, and was reduced to 2 to 5 per cent in another group totaling 16 per cent. The remaining one-fourth of the pastures (24 per cent) presented a cover of 1 per cent or less.

Extremely poor conditions varied with the better ones throughout. The bare soil during periods with moisture is populated with annual weeds, chief of which is Russian thistle. In many places it is only with difficulty that one can distinguish denuded pastures from weedy, tilled land. Cacti have increased greatly almost everywhere and constitute a serious problem.

Because of the low precipitation of 1939, most ranges have lost any gains made during favorable periods since 1934, and further reduction in vegetation seems certain if the winter also is dry.

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# THE PLANT ECOLOGY OF MAUNA KEA, HAWAII [1]

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A study of the vegetation of the sub-alpine and alpine zones on Mauna Kea, the highest mountain in Hawaii (figs. 1 and 2), was made August 6 to 20, 1935, under the auspices of the Hawaiian Academy of Science. Studies were conducted on two slopes of Mauna Kea in the neighborhood of Humuula and Laumaia, with southern and southeastern exposures, respectively. Trips were made also to the upper part of the montane zone above Laumaia and to the lava flows of Mauna Loa below the Humuula Sheep Station. Observations around Laumaia extended in altitude from the *Acacia-Metrosideros* forest at 5,800 feet to the lower part of the alpine zone at 9,600 feet. Observations around Humuula extended in altitude from lava flows at 6,200 feet to the summit of Mauna Kea at 13,784 feet.

This paper gives an account of the plant ecology and floristics of the region. A general account of the Mauna Kea Expedition was published by Wentworth ('35), a geological report by Gregory and Wentworth ('37), and a meteorological report by Coulter ('38). Preliminary reports of the botanical studies have been made by Hartt and Neal (paper presented at the Denver session of the Ecological Society of America in June, 1937) and Neal ('39).

Mauna Kea is an extinct volcano, and it is one of four volcanic mountains that constitute the island of Hawaii. Its rough slopes are cut by canyons, marked by lava flows radiating from its center, and dotted with cinder cones. On the slopes of the mountain between the altitudes 5,000 and 12,000 feet, the gradient

ranges from 500 to 1,500 feet to the mile. A gently sloping plateau makes up the ten square miles of the glaciated, cone-dotted summit. The plateau begins between the altitudes 11,000 and 12,000 feet on the different sides of the mountain, and it rises gradually in a slight dome to a portion 13,000 feet high, where a few large cinder cones standing in a group form the summit of the mountain. The deep soil and weathered rocks found here and there on its slopes give evidence of the great age of Mauna Kea. On the summit and slopes there is also evidence of Pleistocene glaciation, probably the only place in the central Pacific where such a record can be found, according to Gregory and Wentworth ('37). This adds interest to the region both geologically and botanically.

## HISTORICAL SKETCH

The first recorded ascent of Mauna Kea was made by Goodrich (1826), an American missionary. He left Mr. Parker's place at Waimea August 25, 1823, and reached the summit the next day. He noted three or four regions in passing from the seashore to the summit of the mountain: first, five or six miles of cultivated and cultivatable land; then a sandy region, almost impassable, where "brakes, a species of fern, grow to the size of trees, the bodies of some of them 18 inches in diameter"; then a woody region 10 to 20 miles in width; and finally a grassy region where he found strawberries, raspberries "as large as butternuts," and whortleberries, and herds of wild cattle. Later, November 17, 1832, Goodrich (1833) reported finding a lake, 75 rods in circumference, about half frozen over in December.

On June 17, 1825, Macrae (Wilson, '22), botanist of the "Blonde," climbed Mauna Kea and was the first person to
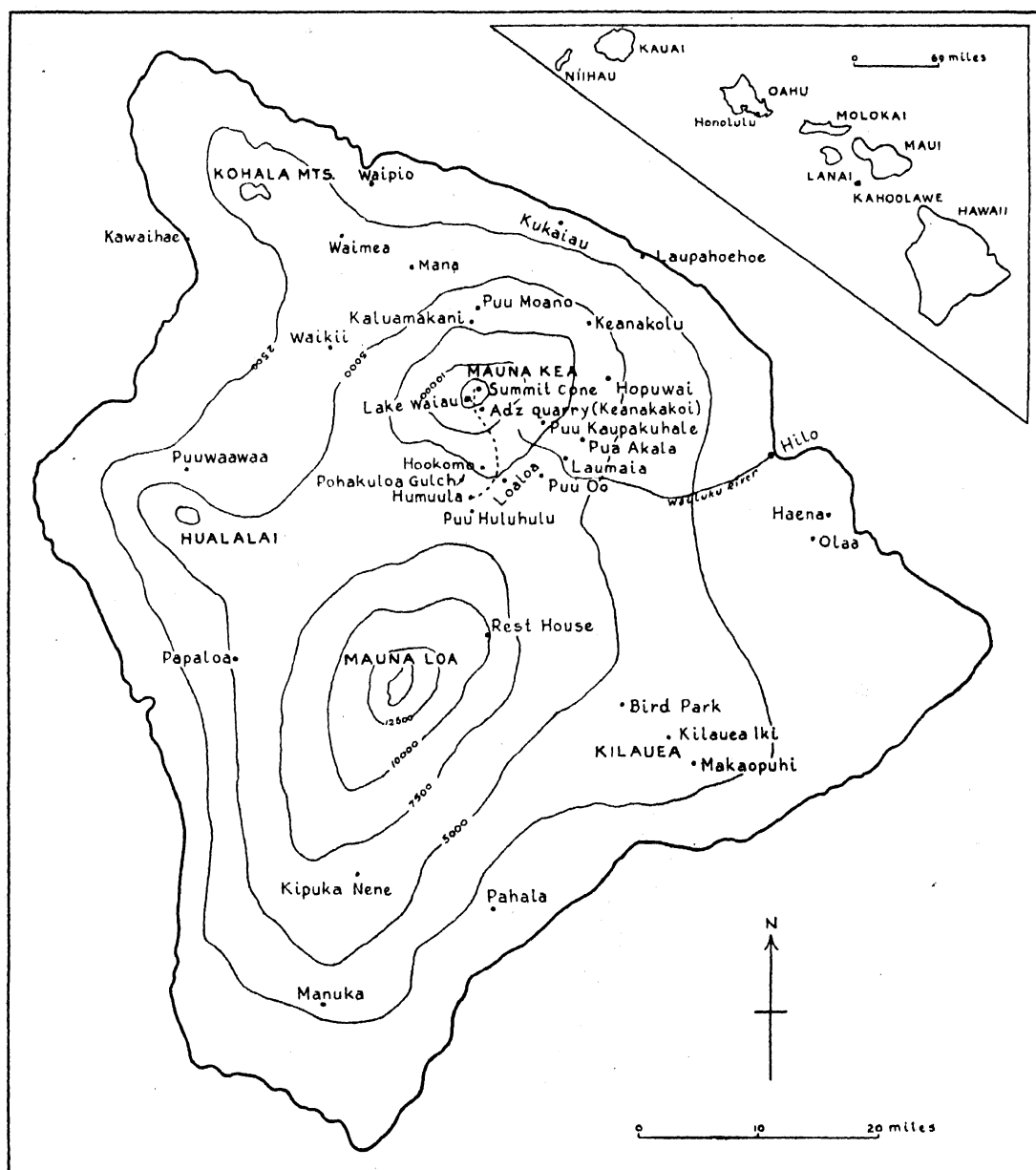
FIG. 1. Sketch map of the island of Hawaii. Inset shows the seven largest islands of the Hawaiian group. All places mentioned in this report are shown on the map.

note the silversword (*Argyroxiphium sandwicense*). His party left Laupahoehoe, at the northeastern base of Mauna Kea, and followed a path up to the woods four miles away. From the coast to six miles inland he found long grass growing "and short stumpy tree ferns belonging to the Cyathea tribe, whose roots afford food for the swine about the huts of the natives." The woods included *Metro-*

*sideros* (some trees reaching a height of 40 feet; some with yellow flowers). *Aleurites, Rhus, Acacia koa,* ferns to 25 feet high, *Psychotria* spp., lobelias; higher up, *Rubus, Fragaria, Sophora,* and *Vaccinium.* Referring to the silversword, he said, "The last mile was destitute of vegetation except one plant of the Syginesia tribe, in growth much like a Yucca, with sharp pointed silver coloured leaves
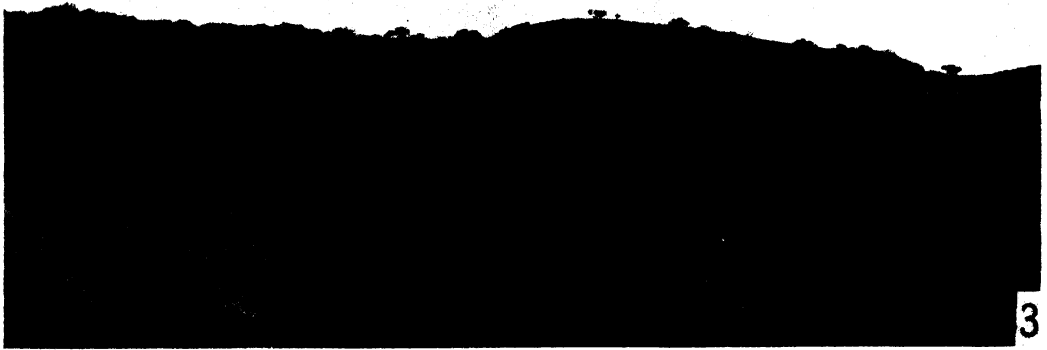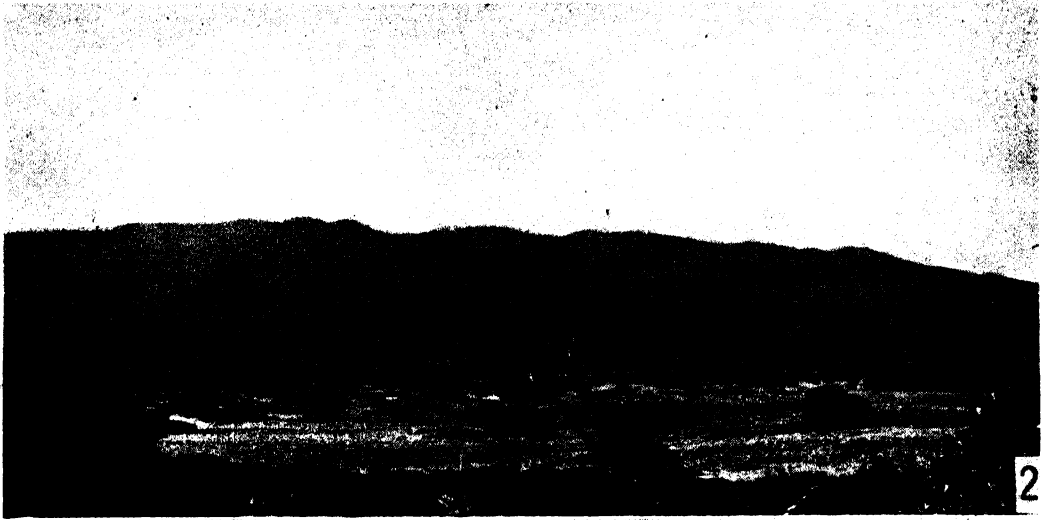
Fig. 2. Mauna Kea from Puu Huluhulu. In right foreground, *Cupressus macrocarpa* surrounding the Humuula Sheep Station; in the pasture, scattered trees of *Sophora chrysophylla*.

Fig. 3. Timberline on south slope of Mauna Kea, altitude 9,500 feet, showing pure stand of *Sophora chrysophylla*.

and green upright spike of three or four feet producing pendulous branches with brown flowers, truly superb, and almost worth the journey of coming here to see it on purpose."

In January, 1834, Douglas ('14) climbed Mauna Kea. He reported that there was no division between the phanerogams and cryptogams, but that the limits of vegetation were defined with the greatest exactness, and the species did not gradually diminish in number and stature. Above the upper limit of the woody country, where the barometric pressure was 21.45 inches, he found *Rubus, Vaccinium, Fragaria,* a few species of grasses and ferns, and some alpine species, and noted the small "*Juncus*" (probably a *Luzula*) and the silversword at greater altitudes than any other plants, and a *Ranunculus* as high as there was any soil.

In January, 1841, Pickering and Brackenridge, members of the United States Exploring Expedition under Captain Wilkes, ascended Mauna Kea. After leaving Hilo they came to the Wailuku River on the southeastern slope of the mountain, passed around to the southern

slope, and evidently reached the summit from that side. Records of the ascent and notes of the plants found were published by Wilkes (1844), Brackenridge (1855), and Gray (1854).

Hillebrand (1888), in a discussion of the zonation of vegetation in Hawaii, placed the upper limit of vegetation for Mauna Kea at 11,000 feet.

On August 6, 1889, Baldwin (1889) left Hilo to climb Mauna Kea on its east flank. From the lower slopes of "fine pasture land," his party reached Pua Akala (altitude 6,300 feet), above which they followed some of the numerous cattle trails through a scattering grove of *Sophora* trees, which " with the exception of a few koa [*Acacia koa*] trees, seems to be the only tree that grows above the regular forest line. Vegetation grows very scarce after leaving Kaupaloihale [possibly Puu Kaupakuhale, altitude 10,-053 feet, is meant], at the foot of which the tree limit ends. Lake Waiau we found to be about 200 by 150 feet. The water was muddy and very stagnant."

Alexander (1892) spent a week on the summit of Mauna Kea, going up by the Humuula trail. He stated that the upper limit of *Sophora* was not far from 10,000 feet, that *Dubautia* extended a thousand feet higher, and that the silversword was nearly extinct. Grasses and ferns were found among rocks by Lake Waiau.

Hitchcock ('17, '22) climbed Mauna Kea in 1906 and published photographs of the timberline region, showing several species of grasses.

Rock ('13) and Hillebrand (1888) named the following as the characteristic trees of the upper forest region : *Sophora chrysophylla, Myoporum sandwicense, Acacia koa,* and *Metrosideros polymorpha. Dubautia arborea* was found up to 10,000 feet and *D. struthioloides* up to 11,500 feet. The silversword was very scarce ; *Senecio vulgaris* was recorded up to 10,000 feet. *Ranunculus hawaiiensis* was exceedingly plentiful, especially above Waikii and in the craters of Kaluamakani and Puu Moano. *Styphelia douglasii* was

very common. *Sonchus oleraceus* was the last plant observed on Mauna Kea, at 12,000 feet, prostrate, with leaves and flowers closely pressed to the ground and with a long rootstock.

Forbes, in 1915, made a trip to the summit of Mauna Kea by way of the Humuula trail, and he noted the plants found. Unfortunately, his altitudinal records are meagre in his field notebook (unpublished).

Kraebel ('22) published a list of plants found on the northeastern slope of Mauna Kea, between Kukaiau and the limit of abundant vegetation at about 10,000 feet.

An interesting study of the flora of the high Hawaiian volcanoes has recently been made by Skottsberg ('31), who noted particularly the poverty of alpine Hawaiian flora. In September, 1922, he reached the summit of Mauna Kea by the Humuula trail. According to Skottsberg, only four phanerogams, all of which are shrubs, deserve to be called " eu-alpine." a subject that will be discussed below. The poverty of alpine species he attributed in part to the fact that the main floristic element in the montane zone is the Paleotropical, which must have been unable to produce alpine species. He suggested that the present alpine flora is at least in part the remainder of an old Hawaiian stock which inhabited lofty summits now worn down to less than 6,000 feet and destitute of alpine species. According to this theory, the descendants from an old mountain flora found refuge on the younger mountains. Skottsberg stated that late oversea immigrants are absent from the alpine zone and that several endemic genera are present.

On May 16, 1923, Neal reached the summit of Mauna Kea, ascending from Kukaiau on the northern slope, along a trail that led through forests of *Acacia koa* and *Sophora,* opening here and there into grassy spots. Higher up, the vegetation decreased and rough lava appeared. *Sophora* trees continued plentiful, also shrubs, particularly *Styphelia,* and tufts of grasses—all growing in both soil and

cinders. Wild sheep were seen. The upper limit of trees was well above 9,000 feet and of other vegetation several hundred feet higher. The Summit Cone was covered deeply with snow, and patches of snow were scattered around the summit area. Lichens on rocks were the only vegetation seen on the summit. Neal descended on the northwestern slope. Before any other plants, many dead stalks of silversword were seen, and the first tree at timberline was a large, twisted *Sophora*. Between altitudes 4,500 and 6,500 feet the party then circled Mauna Kea on the northern and eastern·slopes from a camp near Mana to Puu Oo. The vegetation changed from an abundance of grass and a scattering of trees near Mana to a greater number of *Acacia koa* trees, and farther east to both *Acacia* and *Sophora*, with patches of *Physalis peruviana*, native species of *Rubus* and *R. rosaefolius*. Many herds of cattle were seen. The most luxuriant forest was noted on the northeastern slope, near Keanakolu, altitude 5,400 feet. From Hopuwai southward, the trail led through more open country. Extensive pastures

reached from Laumaia to Puu Oo and beyond, with a scattering of ferns, *Acacia koa*, and *Myoporum sandwicense*.

## PLANT ECOLOGY

*Zonation.*—Schimper ('03), distinguished four world-wide zones of vegetation upon mountains: basal, montane, subalpine, and alpine. These zones correspond to the regions outlined for Hawaii by Hillebrand (1888) and Rock ('13): lower forest zone (basal); middle forest zone (montane); upper forest zone (subalpine). No region corresponding to the alpine zone of Schimper was described by either Hillebrand or Rock.

The upper forest zone of the vegetation of Hawaiian mountains is considered equivalent to the subalpine zone of Schimper because of the well-defined upper limit at timberline (fig. 3), its position above the middle forest region or place of greatest rainfall, the open formation of the trees (fig. 4), and the curious growth forms in the region of the timberline. Examples of the different growth forms exhibited by *Sophora chry-*



FIG. 4. South slope of Mauna Kea, altitude about 8,000 feet, showing *Sophora chrysophylla* in open formation characteristic of the subalpine zone. Photo by C. K. Wentworth.

FIG. 5. Largest *Sophora chrysophylla* found above Laumaia, altitude about 9,500 feet. Dry cinders and scattered rock in foreground.

*sophylla* are shown in figures 5 to 8. Not all the peculiar growth forms of the subalpine zone in such regions as the Rocky Mountains or the Alps are found in the upper forest zone of Mauna Kea, probably because most of the trees exhibiting such forms in temperate regions are gymnosperms; no native gymnosperms grow in Hawaii.

Some of these statements might be questioned, however. The fact that the trees grow in open formation rather than in close stands is undoubtedly influenced by grazing and by low rainfall, particularly on the Humuula side of the volcano. These factors are not so important near Laumaia because of the protection from grazing afforded by the fencing and because the rainfall is about three times that in the region of Humuula. Although some of the curious growth forms may be due to regrowth following grazing, others seem definitely due to wind. The well-defined upper limit at timberline is not questioned; but it is recognized that edaphic conditions and exposure influence the location of the timberline. Because the region dominated by the *Sophora* forest (the upper forest region or subalpine zone) and the region here called the alpine zone differ both climatically and ecologically it is impossible to place

Fig. 6.   Shrubby form of *Sophora chrysophylla*.  Same locality as figure 5.

them in the same category. The main reason for considering the timberline of Mauna Kea climatic rather than edaphic is the severity of the temperature. The arbitrary limit for a climatic timberline is fixed at the mean minimum July temperature of 10° Centigrade. At Lake Waiau, 13,007 feet altitude, the mean minimum temperature in July-August is certainly 0° C. or less; hence at 9,500 feet altitude, the elevation of timberline on Mauna Kea, the minimum mean for July is about 6° C. Coulter ('38) described the

weather at the summit of Mauna Kea as sub-polar throughout the year. In February, 1936, heavy snow fell far below the timberline, and even in summer freezing temperatures are common at night in the alpine zone. Because of low temperatures the growing season is short. The alpine and subalpine zones also differ floristically. *Sophora,* which is the dominant tree in the subalpine zone, is not found at all in the alpine zone. No vascular plants are restricted to the alpine zone. The silversword, popularly be-

lieved to be restricted to the high moun-
tain peaks, grows at altitudes as low as
6,000 feet.   Of Skottsberg's ('31) four
eu-alpine species, two were not found on
the Mauna Kea Expedition: *Tetramolo-
pium arbusculum* (= *T. chamissonis* var.
*arbuscula*), from eastern Maui only, and
*Dubautia struthioloides* (= *Raillardia
struthioloides*) ; and two have been re-
corded from places as low as 4,000 feet :
*Geranium cuneatum* var. *hololeucum* (=
var. *pauciflorum*) and *Vaccinium pele-
anum*.   (See List of Plants at the end of
this report.)   The absence of any species
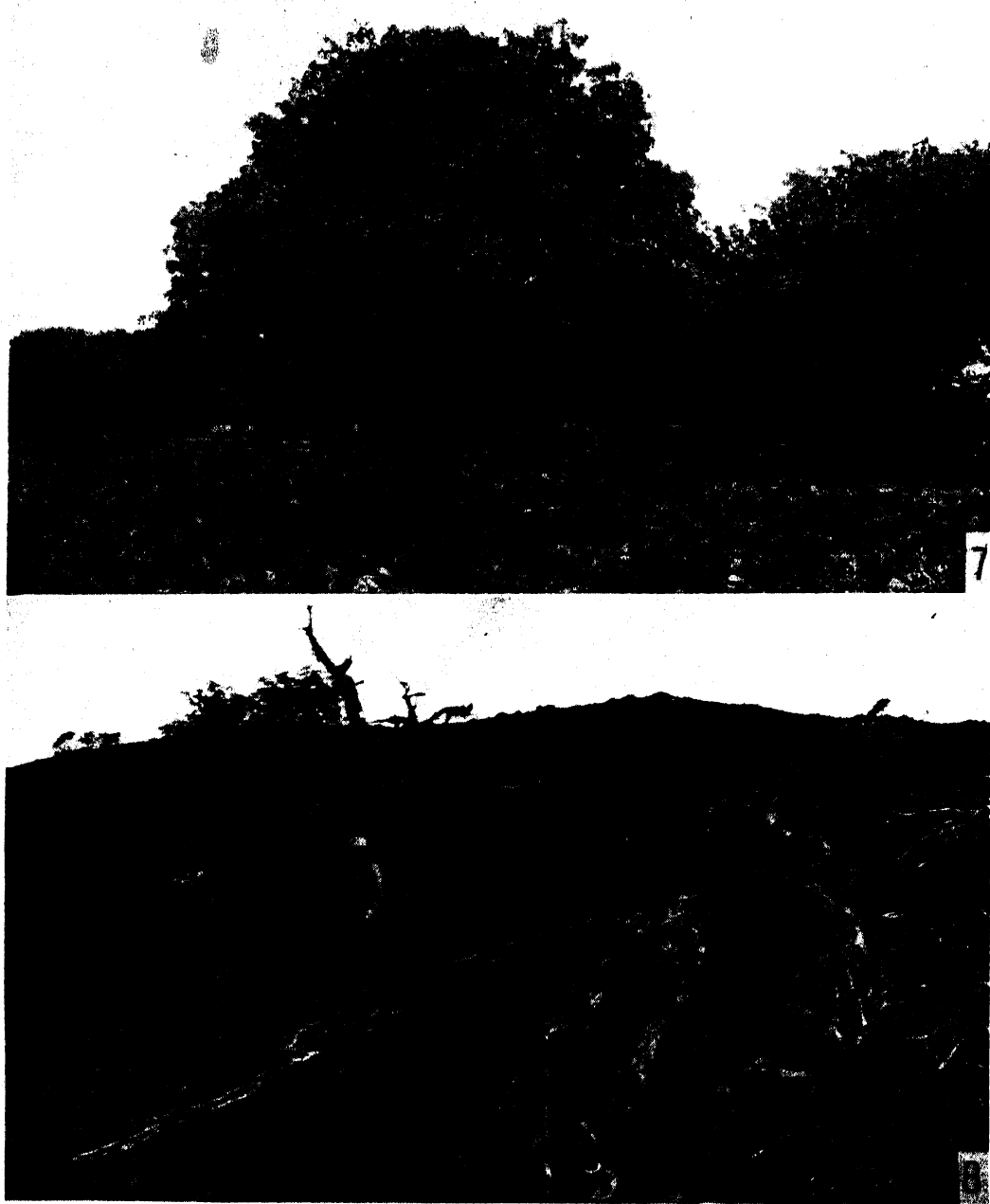


FIGS. 7 AND 8.  Growth forms of *Sophora chrysophylla* found above Laumaia.  Fig. 7.
Symmetrical form in park-like setting in typical association with *Pteridium aquilinum*, altitude
8,550 feet.  Fig. 8. Sprawling form, nearly dead, altitude 9,500 feet, at timberline.
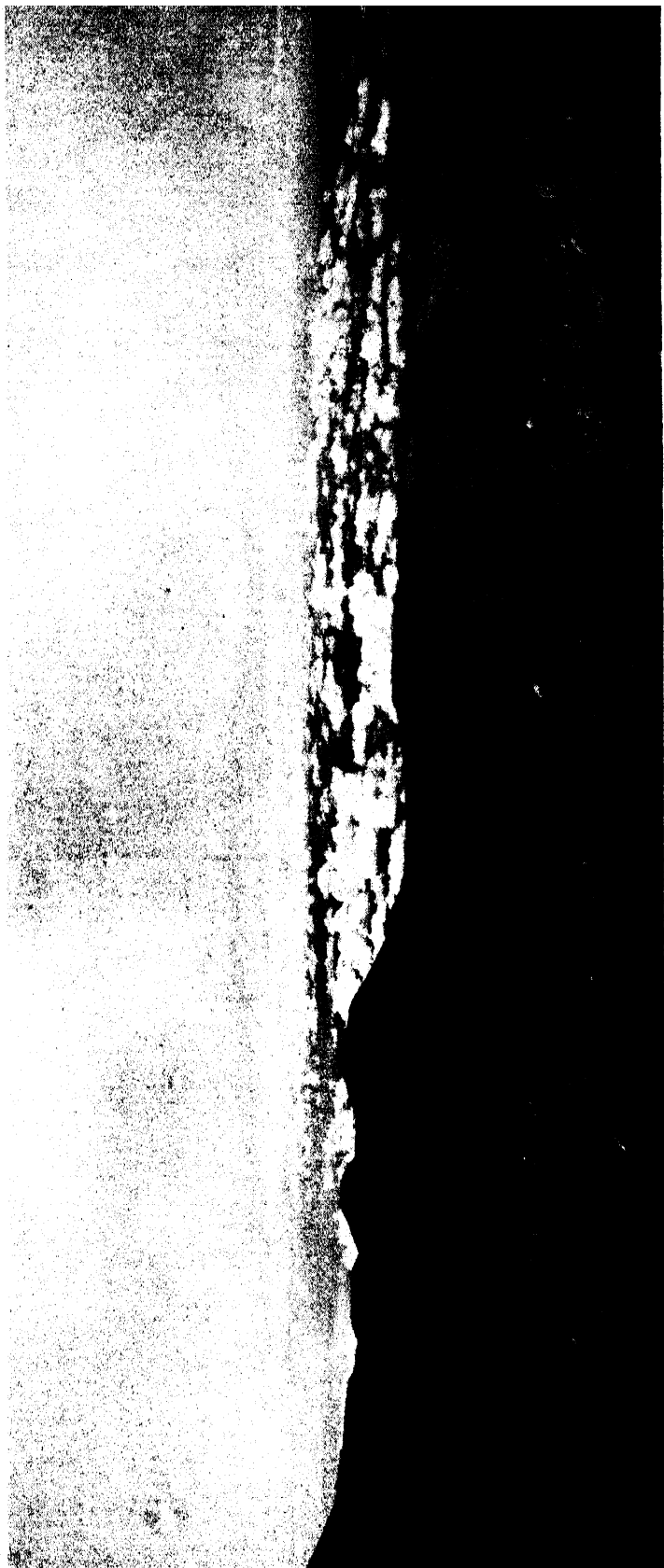
Fig. 9. View from summit of Mauna Kea, an alpine desert; lower slope of Mauna Loa at right. Photo by C. K. Wentworth.

Fig. 10. Cinder cones on the summit of Mauna Kea. Location of highest vascular plant on left rim of right cone. Photo by Inter-Island Airways, May 12, 1933.

confined to the alpine zone is an insufficient reason for considering the alpine zone as non-existent, because their absence may be explained in other ways. Mauna Kea, located on an oceanic island which, according to the geologists, was never connected with continental areas, was therefore never in a position to receive migrating arctic-alpine plants during glaciation as did the Rocky Mountains and other highlands in temperate regions. The glaciation of Mauna Kea destroyed any vegetation previously present, and since the glaciation period the only source of plants for the summit region (other than chance introduction by high air currents) is the lower slopes of the mountain. Therefore, it is not strange that the plants found in the summit region of Mauna Kea are also found below. The theory of Skottsberg ('31) that the present alpine flora has come from the former more lofty summits awaits confirmation.

Without question, the alpine zone on Mauna Kea belongs in the category of alpine deserts (figs. 9 and 10). Very few species and very few individual plants are found. The landscape is completely determined by the substratum; the vegetation is subsidiary. The alpine zone of Mauna Kea is classed as alpine because of its ecological characteristics; there are no upright tree trunks, in fact no trees at all. The growth forms include lichens, bryophytes, low shrubs, rosette plants, and small diffuse herbs. Some of the characteristics of alpine zones elsewhere are absent. None of the flowers have brilliant colors with the exception of the dandelion, an introduced weed. The plants found blooming in the alpine zone were *Styphelia douglasii, Taraxacum officinale, Tetramolopium humile* var. *skottsbergii,* and five grasses: *Agrostis sandwicensis, Anthoxanthum odoratum, Poa annua, P. pratensis,* and *Trisetum glomeratum* (fig. 11). No investigation was made of the size of the underground parts of the alpine plants. The plants were so scarce that it was felt none should be disturbed except the few needed for taxonomic study. The long rootstock of *Sonchus oleraceus,* the highest plant on the mountain observed by Rock ('13), at




FIG. 11. *Trisetum glomeratum,* in the alpine zone, altitude about 13,000 feet. Photo by C. A. Poutre.

FIG. 12. Highest specimen of *Styphelia douglasii* found on Mauna Kea, altitude 10,500 feet.

12,000 feet, is an example of the large underground parts characteristic of alpine vegetation, and the plant's prostrate growth, with leaves and flowers closely pressed to the ground, shows that it had the typical growth form of the alpine zone. No tree mats were seen, but the three living specimens of the introduced scrub pine, *Pinus contorta,* which had been planted in the fenced enclosure by Lake Waiau, were only six to eight inches in height.

Of the species of shrubs, *Coprosma ernodeoides* and *Styphelia douglasii* might be considered to form shrub mats. However, the form of *Coprosma* is not due to the alpine climate, inasmuch as the natural growth-form of the plant is a shrub mat even at low altitudes. *Styphelia douglasii* does not form extensive mats but did cling closely to rocks in places and was decidedly dwarfed at the higher altitudes, approaching the cushion habit (fig. 12). Several plants had the rosette growth form: *Argyroxiphium sandwicense, Cirsium vulgare, Luzula hawaiiensis, Ranunculus hawaiiensis, Rumex acetosella, Senecio sylvaticus,* and *Taraxacum officinale.* No true cushion plants were found, though the growth form of *Tetramolopium humile* var. *skottsbergii* resembles a cushion.

One of the characteristics of the alpine zone is a shorter growing season than that at lower altitudes, a condition that is reflected in the flowering of the plants. The following plants were found in flower in the subalpine zone but not in the alpine zone: *Gnaphalium japonicum* and *G. sandwicensium, Coprosma ernodeoides, Geranium cuneatum* var. *hololeucum, Dubautia arborea,* and *D. ciliolata* var. *juniperoides.*

To sum up, the alpine characteristics noted on Mauna Kea are as follows: the absence of upright trees, the presence of rosette plants and quasi-cushion plants, a dwarfing in size of the plants, and the absence of flowers on some of the plants which were in bloom at that time at lower altitudes. A total of 31 species of ferns and flowering plants were found above the timberline.

The upper limit of the alpine zone is the upper limit of vegetation and it is interesting to note the upper limits of distribution of various species of plants within this zone. *Pellaea ternifolia* was seen in a rock outcrop at 10,400 feet altitude; *Styphelia douglasii* at 10,500 feet, on the Humuula trail (fig. 12), and *Styphelia* sp. at 11,600 feet in Pohakuloa Gulch. The only plant of *Argyroxiphium sandwicense* (fig. 13) was growing upon a rocky shelf in a position well protected from grazing animals, and with it *Vaccinium peleanum,* at 12,250 feet altitude, the highest position at which any shrub was found. Of the grasses, *Agrostis sandwicensis* was recorded at 13,100 feet, and *Trisetum glomeratum* (fig. 11) at 13,400 feet on the east side of the Summit Cone, growing upon rock. Among the rocks on the northeast rim of the Summit Cone (fig. 10), a specimen of *Asplenium adiantum nigrum* was found by C. S. Judd, forester of the Expedition, at 13,500 feet. This was the highest elevation at which any vascular plant was seen, and exceeds the records of Skottsberg ('31), who placed 4,000 meters (13,120 feet) as the upper limit for vascular plants in Hawaii. The summit is marked by a monument formed on a survey, upon which were the highest living plants collected, yellow and orange lichens. Thistledown without seed, from *Cirsium vulgare,* was noted floating in the air above the mountain. Living plants, though scarce, were thus growing far above 11,000 feet, the altitude considered by Hillebrand as the upper limit of vegetation upon Mauna Kea.

*Climatic factors.*—Precipitation is the chief climatic factor affecting the vegetation in the subalpine zone of Mauna Kea. An illustration is the unequal abundance of vegetation on the various sides of such a cinder cone as Puu Huluhulu (fig. 14), and the enhancement of the growth of grass under trees due to the condensation of the fog. The denser vegetation on the

Fig. 13.   *Argyroxiphium sandwicense,* near Humuula trail, altitude 12,250 feet.   Photo by W. P. Naquin.

Fig. 14.   Puu Huluhulu, left slope showing effects of moisture-laden trade wind.

Laumaia side of the mountain as compared with Humuula is at least partly due to the greater rainfall.

Other climatic factors that control the growth of plants in the alpine zone are the shortness of the growing season, low night temperatures in summer, and low precipitation.   Snow has been seen on Mauna Kea in June and August.   In August, 1906, Hitchcock ('17) found a snowbank six feet deep on the summit of Mauna Kea.   On May 16, 1923, much snow was present, and on May 12, 1933, little snow was present (fig. 10).   In August, 1935, we found no snow.   The time of the first snow as well as the amount varies in different years.   Most plants found at lower elevations are un-

able to grow and reproduce and thus establish themselves in the alpine zone because of the short season.

The recorded day temperature is high enough for growth but at night the temperature is below the freezing point, even in the middle of August. This suggests an interesting problem in the physico-chemistry of the saps of the plants. The plants must have considerable resistance to low temperatures and yet be able to conduct photosynthesis during the day.

The low precipitation and the porosity of the substratum cause the greater part of the summit area to be xerophytic. Undoubtedly a most important factor causing the sparcity of the vegetation is the drought. No wonder most of the plants possess definitely xerophytic structures. The most conspicuously xerophytic habit is that of *Argyroxiphium sandwicense* (fig. 13) with its succulent leaves, the grooves of which may intercept rainfall. The awl-shaped, stiff leaves of *Styphelia* (fig. 12) seem xerophytic and may resist rapid transpiration. The leaves of *Vaccinium* and *Asplenium adi-* *antum nigrum* are somewhat leathery. The leaves of *Tetramolopium* have a reduced area and are villous with curly white hairs. *Argyroxiphium sandwicense* is the most unique xerophytic plant in the alpine zone.

Wind may be of importance in the distribution of seeds and thus in the introduction of plants into the alpine zone and may explain the relatively large number of ferns there. However, wind dissemination has not been successful with *Cirsium vulgare;* although thistledown was seen floating in the air only a few plants were found in the alpine zone. The effect of wind upon the shapes of plants was most pronounced with *Styphelia douglasii* (fig. 15).

*Edaphic factors.*—The edaphic conditions are of great interest in both the sub-alpine and the alpine zones. The substrata include aa (rough lava) in various states of decomposition, loose cinders, some areas covered with bombs, soil, and perhaps other materials. In general the topography is youthful, the volcanic constructional forms being little modified.



Fig. 15. *Styphelia douglasii* at timberline on Mauna Kea, altitude 9,500 feet, showing effect of prevailing wind. Photo by C. K. Wentworth.

Small streams and gullies in the subalpine zone generally have a vegetation differing from that of the upland because of greater mesophytism and of protection from grazing animals. Stability of the substratum seems to be a very important factor, more plants generally being found on disintegrating rocks than on the cinders, in the subalpine zone. *Sophora*, however, seems to be able to grow as well in the cinders as upon the soil-covered rocks. Possibly its roots gain a deeper anchorage, reaching a stable stratum, which many herbs are unable to do.

The edaphic factors in the alpine zone of Mauna Kea are very unfavorable for plant growth. The instability of the cinders leads to the destruction of the roots. The porosity of the cinders as well as the lavas makes the substratum dry. The absence of organic matter also gives a low water-holding capacity to the substratum. The formation of soil has hardly begun; in the alpine zone most of the substratum is not soil but parent material, both the cinders and the lavas, glaciated and non-glaciated. The absence of soil renders anchorage difficult, gives an extremely low water-holding capacity and may make it difficult for plants to obtain the mineral elements essential for growth. The edaphic factors combined with precipitation are responsible for the xerophytic character of the habitat, in both the subalpine and the alpine zones (fig. 9).

*Biotic factors.*—The biotic factor of greatest importance is grazing. Formerly more flourishing forests covered larger areas and extended to lower altitudes. The late C. S. Judd, Territorial Forester, who has worked to save Hawaiian forests from destruction by grazing animals, discussed this situation ('36). In 1793 the first cow and bull were landed on the island of Hawaii, at Kawaihae, and were released under a ten-year protective law. They increased rapidly to thousands, and in 1822 they were living in wild herds on Mauna Kea as observed by Goodrich.

In 1856 they were so numerous and harmful to vegetation that Hillebrand, according to Judd, wanted them removed. In 1931 they were removed from upper Mauna Kea. Not only wild cattle but wild goats, sheep, horses, and hogs were offenders. By denuding the ground they caused the formation of erosion gulches. Horses were introduced in 1803, and wild ones lived on Mauna Kea until 1932, when they were removed from the upper slopes. Sheep were caught by wild dogs until the dogs were removed; by 1935 they had increased to 40,000. Sheep, largely, have prevented the development of *Sophora* seedlings. In 1909 the Government made upper Mauna Kea a forest reserve, which by March 1936, included 85,000 acres. In January, 1937, a fence 55.5 miles long was completed, encircling Mauna Kea between altitudes 6,000 and 8,000 feet and protecting 88,108 acres of the summit area from sheep, cattle, and hogs. In August 1935, we saw very few seedlings or young trees, but many old and dying trees. During the Expedition, the seeds of the *Sophora* were found to be widespread, and they should be able to renew the forest now that grazing animals have been removed and their inroads prevented by fencing.

In the alpine zone, grazing has destroyed many plants of *Argyroxiphium sandwicense*. Insect injury to the silver-sword plants, which was observed in the crater of Haleakala in the summer of 1933, was not noted on Mauna Kea. Pack animals going to Lake Waiau are undoubtedly responsible for the dispersal of weeds.

*Plant succession.*—The succession of vegetation upon the lava flows of Mauna Loa at about 4,500 feet altitude was studied by Forbes ('13). On the Mauna Kea Expedition three main types of virgin substrata were encountered in the subalpine zone: aa, pahoehoe, and cinders. The type of succession on all of these substrata is in general xerarch. Aa and

pahoehoe[2] flows of Mauna Loa have overlapped the lower slopes of Mauna Kea and afford interesting contrasts in vegetation, a condition which was studied near Puu Huluhulu at an elevation of about 6,400 feet. Ecological studies of aa flows were also made at several elevations on Mauna Kea. The aa and pahoehoe flows of Mauna Loa studied in this investigation were covered by fresh lava in November, 1935.

Probably the youngest aa flow studied in this investigation was that in the vicinity of Puu Huluhulu where much of the rock was bare. One of the first pioneer plants noted was a gray moss, *Rhacomitrium lanuginosum* var. *pruinosum*, which like other pioneer mosses aids in the development of humus. Because very little soil has formed on these lava flows and because of the dryness of the habitat due to the porosity of the rock, the conditions are unfavorable for the growth of plants and hence for succession. Contrasting with the higher, more exposed parts the irregular depressions in the lava harbored a variety of plants including: *Dryopteris paleacea, Pellaea ternifolia, Carex wahuensis,* and *Tetramolopium humile* var. *skottsbergii.*

Without question the growth of these plants in protected places speeds up the processes of succession by producing moisture-holding humus which facilitates the development of shrubs and trees. On the Mauna Loa flow the chief shrubs were *Styphelia douglasii* and *Vaccinium reticulatum,* and the only tree seen was *Metrosideros collina* subsp. *polymorpha.* Thus the aa flows of Mauna Loa near Puu Huluhulu were progressing from the stage of pioneer mosses, through a stage dominated by native herbs, then shrubs, to a forest of *Metrosideros.* This is an example of primary xerarch succession.

The aa flows of Mauna Kea between the Humuula Sheep Station (altitude

6,784 feet) and timberline (altitude approximately 9,500 feet) are passing through two types of plant succession; those in the pastures are dominated by such introduced herbs as: grasses, *Trifolium* spp., *Rumex acetosella, Taraxacum officinale, Leontodon autumnalis,* and *Cerastium vulgatum;* those in less grazed regions are dominated by such native herbs as: *Gnaphalium* spp., *Pellaea ternifolia,* and *Hesperocnide sandwicensis.* The lava flows now dominated by introduced herbs if left untouched might eventually develop a forest; under present conditions they will probably not reach a forest stage but develop into grassy pastures. The lava flows now dominated by native herbs also support native shrubs, such as, *Styphelia, Vaccinium, Dubautia,* and *Chenopodium oahuense;* and the tree is *Sophora.* Indeed it would seem that the last strongholds of the native plants in the grazed regions of the subalpine zone are the aa flows. With adequate fencing, these lavas should eventually support a forest dominated by *Sophora,* with *Coprosma montana* (fig. 16) subsidiary. At lower elevations such a forest would be dominated by *Acacia koa* var. *hawaiiensis,* which was found in old aa flows, volcanic ash, and other substrata of Mauna Kea, where it was accompanied by *Dryopteris paleacea* (fig. 17).

The only pahoehoe studied in this investigation was that of a lava stream in the vicinity of Puu Huluhulu. Here the smooth surface of the pahoehoe is broken by cracks along which crevice plants grow, by deep depressions, by caves or tunnels, by fallen roofs of lava domes, and by pools. Such a variety in habitat has led to a variety in plant cover. The swirls and crevices in the lava were the habitat of *Coprosma ernodeoides, Styphelia douglasii, Vaccinium reticulatum, Asplenium adiantum nigrum, Pellaea ternifolia, Dryopteris paleacea, Sisyrinchium acre,* and *Tetramolopium humile* var. *skottsbergii,* and several other kinds of plants. Caves both large and small were more moist than the unbroken stretches

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[2] *Aa* is a lava whose surface is rough and scoriaceous in contrast with *pahoehoe,* whose surface is smooth.

Fig. 16.  *Coprosma montana* var. *typica*, on aa flow, hilltop above
Hookomo, altitude 8,000 feet.

of lava and consequently became the habi-
tat of other kinds of plants.  In a deep
cave formed by the breaking open of one
end of a lava tube, the shade, the moist
and dripping walls, the slight evaporating
power of the air, and protection from
grazing animals afforded by masses of
broken slabs of rock, favored plant
growth entirely different from that upon
the unbroken lava flows.  At the mouth
of this cave there was *Rubus hawaiiensis*.
Several ferns, including *Dryopteris
paleacea* and *Polypodium hookeri* (a very

narrow form), were growing farther
within the cave in a place where for
much of the day there is no direct
sunlight.  Still farther within the cave,
well out of the reach of any direct sun-
light and exhibiting marked phototropism,
grew another fern, *Asplenium rhomboi-
deum*.  The walls, floor, and ceiling of
the cave were lined with mosses and liver-
worts.  The presence of such caves prob-
ably hastens succession toward a forest
cover.  Roots may act mechanically and
chemically upon the rocks, causing disin-

tegration, attacking not only the surface but also along the walls and floor of the cave. The mesophytic vegetation within the cave speeds up the development of humus, thus enriching the soil. For these

reasons as well as because of protection, many clumps of *Sophora* trees are found near piles of broken rock which may represent the remains of old caves.

Pools also hasten soil formation upon



Fig. 17. *Acacia koa* var. *hawaiiensis* and *Dryopteris paleacea,* near Puu Oo, altitude 6,300 feet. Photo by C. K. Wentworth.

Fig. 18. Pool in pahoehoe flow from Mauna Loa near Puu Huluhulu, altitude 6,200 feet.

lava flows. These may develop where caves have collapsed overlying rather impervious Mauna Kea gravel. The plants growing in one such pool (fig. 18) included *Heleocharis obtusa* var. *enotata, Carex sandwicensis, Agrostis retrofracta, Hydrocotyle verticillata,* and algae. The accumulation of humus in such pools may hasten the time when trees can be supported.

The only trees on the pahoehoe flows were *Sophora,* contrasting sharply with the aa flows, where *Metrosideros* was the only tree at that altitude. *Sophora* also grows in a wide range of habitats, including pasture lands and aa flows near Hookomo and at higher elevations.

The landscape of Mauna Kea is punctuated with cinder zones. The slopes of many of the cinder cones are nearly bare of vegetation and others are well covered with plants. Although the cinders are unfavorable for the growth of plants, yet the cones do eventually become clothed with vegetation, as at Puu Huluhulu (fig. 14).

Just what the pioneer plants are upon the cinder cones is not apparent from this study. There were no lichens or mosses upon the cinders, but some of the bombs scattered over the surface of the cinders were partly covered with small crustose lichens. *Styphelia* is able to grow in the cinders, and under it herbs find a foothold, whereas between the plants of *Styphelia* there are bare areas, suggesting either that *Styphelia* may be the pioneer plant or that it grows only in locations already stabilized by the presence of herbs.

Whatever the pioneer plants, the distribution of the vegetation upon the cinder cones is influenced markedly by their exposure to clouds and fog. One cone was noted which was bare of vegetation in the lower half, from which the moisture-laden winds were cut off by a neighboring cone; the upper half of this cone was partly covered with *Styphelia douglasii.* This plant was found at an altitude of 6,400 feet, our lowest station for that species.

Puu Huluhulu, a small cinder cone of Mauna Kea, reaching an elevation of about 6,700 feet, located below the Humuula Sheep Station, is entirely surrounded by Mauna Loa lava flows, which separate it from the pastures. There was much greater floristic difference between Puu Huluhulu and the lava flows than between the aa and pahoehoe. Possibly the vegetation upon Puu Huluhulu constituted a remnant of a forest formerly more widespread in the region now covered with pastures at that altitude. The east side of the cone derived greater benefit from the trade winds than the other side of the cone, resulting in a conspicuous difference in density of vegetation. The trees upon the cone were *Acacia koa* var. *hawaiiensis* and *Myoporum sandwicense,* which probably constitute the climax stage. Mosses, lichens, *Panicum tenuifolium, Epilobium oligodontum,* and *Sisymbrium officinale* constituted the undergrowth.

In addition to the cones, much of the area between the Humuula Sheep Station and timberline and above Laumaia consists of cinders. Two types of plant succession were distinguished in this region: secondary succession leading to the climax forest of *Sophora,* and retrogression in the *Sophora* forest due to overgrazing. Probably little primary succession is taking place now. Enough time has elapsed since the formation of the cinders for the growth of a *Sophora* forest where climatically possible, with the exception, of course, of new areas, such as gullies. Present changes are chiefly either retrogression or a return to the *Sophora* forest.

One of the principal evidences of retrogression was the presence of many dead *Sophora* trees (fig. 8). Some have died from natural causes but others have been barked by wild goats or uprooted by wild sheep. Because of overgrazing, the dryness of the region, and instability of the cinders, very few herbaceous plants were able to grow. Large areas above Hookomo were characterized by dead and dying *Sophora* trees and the complete ab-

sence of undergrowth; in other places the *Sophora* trees were not yet injured but the undergrowth was very thin. An introduced grass, *Poa annua*, was found in round areas of turf. This and other grasses grew especially under the trees, receiving moisture intercepted and condensed by the trees. Other herbs in that region were *Pteridium aquilinum*, *Arenaria* spp., *Cirsium vulgatum*, *Erigeron linifolius*, *Erodium cicutarium*, *Gnaphalium* spp., *Leontodon autumnalis*, *Lepidium virginicum*, *Oxalis corniculata*, *Rumex acetosella*, *Senecio sylvaticus*, *Taraxacum officinale*, *Trifolium* spp., mosses, and lichens. Some of the herbs, ·mosses, and lichens were epiphytic upon the *Sophora* trees (fig. 19).

Near the Humuula Sheep Station, there were only a few scattered *Sophora* and *Metrosideros* (fig. 20) trees in the pastures. Due chiefly to the greater precipitation, excellent pasturage has devel-



FIG. 19. Epiphytes on *Sophora chrysophylla*, including mosses, lichens, and *Polypodium lineare*, altitude about 7,000 feet. Photo by C. K. Wentworth.

oped, consisting of both native and introduced herbs, including the following: *Centaurium umbellatum*, *Luzula hawaiiensis*, *Achillea millefolium*, *Chenopodium oahuense*, *Erodium cicutarium*, *Gnaphalium* spp., *Lepidium virginicum*, *Rumex acetosella*, *Sisymbrium officinale*, *Taraxacum officinale*, *Trifolium*, mosses, lichens; and the following grasses: *Agrostis retrofracta*, *Bromus mollis*, *Danthonia pilosa*, *Deschampsia nubigena*, *Festuca dertonensis*, *Hordeum murinum*, and *Panicum tenuifolium*. If left ungrazed these pastures might in time return to a *Sophora* forest, since there were scattered trees producing seed. Under the present conditions of grazing they will more probably continue as grasslands.

Regarding the succession of vegetation in the alpine zone even less can be said than about that in the subalpine zone.

Hydrarch succession in Lake Waiau must be exceedingly slow. The presence of ice on the water every morning even in early August renders the growth of any plants very slow, to say nothing of a progressive change from one type of vegetation to another. No aquatic plants except algae (fig. 21) were found and these formed a luxuriant growth around the edge of the lake, especially on the north side. Whether submerged and emergent aquatic plants will ever reach Lake Waiau by a natural means of dissemination, or whether they could grow there if introduced, are purely speculative problems. The plants living in Lake Waiau have been described by Neal ('39).

Xerarch succession on the rocks in the summit area, if occurring at all, is also very slow. Several kinds of lichens were found, none of which were abundant. The commonest herbs were *Asplenium adiantum nigrum* and *Trisetum glomeratum*, which were generally found in protected cracks and under the edges of the rocks. More species of plants were found in Waiau Crater than elsewhere in the summit area, probably because that is the chief destination of pack animals and because of the moisture from melting

snow. In addition to the fern and grass just named, the following plants were found near Lake Waiau upon a rocky terrain: *Stellaria media, Cirsium vulgatum, Erigeron linifolius, Taraxacum officinale, Poa annua,* and *P. pratensis.*

A census was taken of the plants in the area enclosed by a fence (fig. 21), located in the crater of Lake Waiau. The enclosure was 46 by 43 paces. No planted trees labeled *Juniperus* or *Picea* were found alive; three living specimens
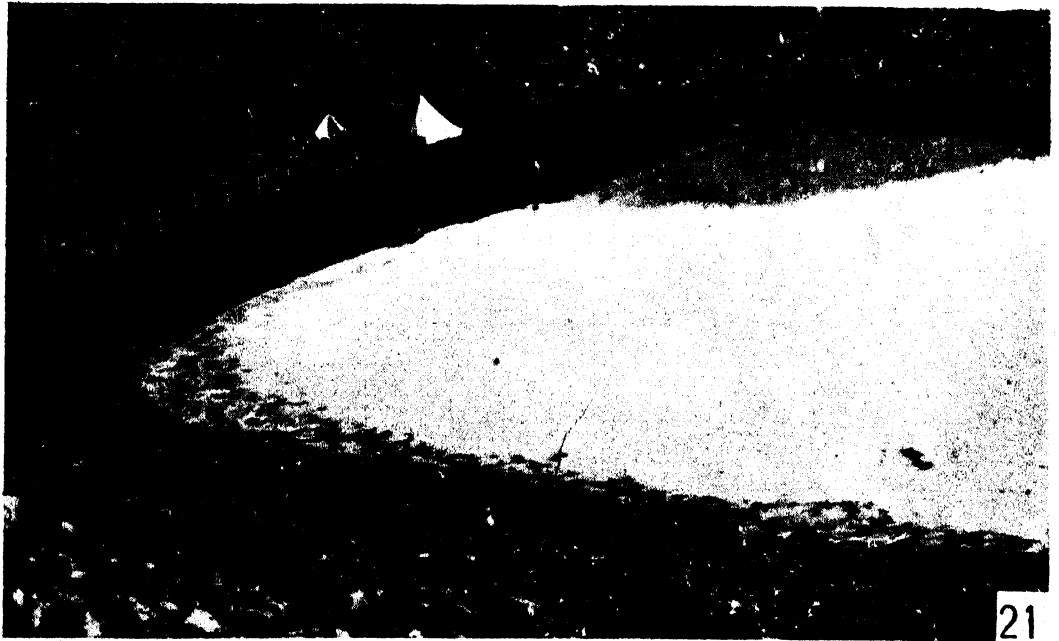




Fig. 20. *Metrosideros collina* subsp. *polymorpha* in pasture at Humuula, altitude 6,700 feet.

Fig. 21. Lake Waiau, Mauna Kea, altitude 13,007 feet, showing the camp of the Expedition, fenced area, and algae fringing the lake. Photo by W. P. Naquin.

of *Pinus contorta* were found, all very short (6 to 8 inches in height). The following numbers of plants were found: *Cerastium vulgatum*, 310+; *Trisetum glomeratum*, 260+; *Taraxacum officinale*, 122+; *Rumex acetosella*, 42; *Anthoxanthum odoratum*, 39; *Poa annua*, 25; *Poa pratensis*, 23; *Cirsium vulgare*, 1. *Cerastium vulgatum* and *Rumex acetosella* were confined to the lower half of the plot; the other plants were well distributed.

One may safely say that the entire summit area which bears any vegetation at all is in the pioneer stage. To study succession in the summit area of Mauna Kea one would probably need to return every 500 years.

Because only pioneer lichens, mosses, and herbs were found in the summit area, the planting of gymnosperm trees in that region is almost certainly doomed to failure. Such plants do not grow in the alpine zone of their native territory, except as mats in mesophytic habitats, and then only where there is at least a little soil. The Hawaiian Islands, never having been connected with mainland areas according

to geologists, were not in a position to receive migrating arctic-alpine plants. The introduction of some alpine xerophytic herbs from the Rocky Mountains and elsewhere, as *Silene acaulis, Phlox canescens*, or *Anemone globosa*, might yield interesting results.

Comparison of vegetation showed that plants in the *Sophora* forest on the Laumaia side were larger than those on the Humuula side. Larger plants of *Dubautia* (fig. 22) were found on the Laumaia than on the Humuula side. The vegetation was richer in native species at Laumaia and richer in introduced plants at Humuula.

## FLORISTICS

The plants collected by the Mauna Kea Expedition include bacteria, algae, fungi, lichens, mosses, liverworts, ferns, and spermatophytes. They were obtained at altitudes of 5,800 to 13,784 feet, except one species, *Cirsium vulgare*, which ranges down to 5,000 feet. The following list includes mosses, ferns, and flowering plants, which total 146 species and



FIG. 22. *Dubautia ciliolata* var. *juniperoides* in *Sophora* forest above Laumaia, altitude about 8,750 feet.

varieties. Fungi, lichens and liverworts have not yet been studied. The list shows that the altitudinal range of certain species is greater than that previously reported. Thus, nine mosses were found at altitudes 1,800 to 3,900 feet higher than previously recorded, and two other mosses in the alpine region only. As compared with earlier records, four ferns were found at altitudes 1,300 to 2,600 feet higher and 29 spermatophytes at altitudes 1,000 to 10,000 feet higher. These extensions in range indicate the need of more comprehensive and more accurate study of the vegetation of the Hawaiian mountains. Two species and one variety of spermatophytes are newly recorded from Mauna Kea: *Arenaria leptoclados, A. serpyllifolia, Peperomia cookiana* var. *minutilimba. Asplenium rhomboideum,* found only on Haleakala, according to Hillebrand, and collected by Forbes on Hualalai and Mauna Loa, and by Rock and Newell on Mauna Kea, was collected again on Mauna Kea. *Geranium multiflorum* var. *typicum,* found at Loaloa at an altitude of about 7,000 feet by R. L. Usinger, one of the entomologists of the Expedition, had not been collected since the Wilkes Expedition, nearly one hundred years ago. With the exception of the bacteria, the specimens have been deposited in the Bernice P. Bishop Museum.

For the collection of bacteria, sterilized agar tubes furnished through the courtesy of C. W. Carpenter, of the Experiment Station of the Hawaiian Sugar Planters' Association, were exposed to the air of Lake Waiau and on the Summit Cone. Others were inoculated with samples of spring water, lake water, glacial rock, and cinders in the summit area. The microorganisms that developed in these tubes were given to Prof. O. N. Allen of the University of Hawaii for identification.

Allen (personal communication) reported that nothing in the way of new species or uncommon forms of bacteria were found in the tubes. In fact, the types and kinds of organisms which developed in the tubes were quite compar-

able with those found on Mount Tantalus, altitude about 2,000 feet; Punchbowl, altitude about 500 feet; and similar areas on the island of Oahu. The tubes inoculated with air and spring water were found to be sterile. This, however, does not prove the complete absence of microorganisms from the air and the spring water, because standard methods of examination require petri dish exposure rather than the test tubes used in this investigation. However, since the same method was used with both spring water and lake water, it is interesting to note the development of microorganisms inoculated with lake water and the absence of such development in the tubes inoculated with spring water.

Additional information is given in a letter written by Dr. H. L. Lyon to Gregory ('37) : " The water from Waiau Lake is a veritable infusion. Bacteria are extremely numerous and probably the chief factor in causing the turbidity of the water. A small ciliate is also present in enormous numbers, while a larger infusorian, *Stylonychia* sp., is present in large numbers. I also find a few diatoms and numerous dead bodies of a crustacean, *Daphnia* sp. which are being consumed by a fish mold, *Achlya* sp. The sample of muck contains several bluegreen algae, desmids, diatoms, at least two species of nematodes, hosts of bacteria and many kinds of protozoa, among which are present all of those found in the sample of water."

Algae, collected in three places, were determined by J. T. Koster. Near Puu Huluhulu, in a shallow pool in a depression on pahoehoe (fig. 18), altitude 6,200 feet, *Nostoc entophytum* Born. et Flah., *Stigonema minutum* (Ag.) Hass., and *Haematococcus pluvialis* Flotow em. Wille were collected. At Humuula, altitude 6,700 feet, on the bark of *Cupressus macrocarpa,* *Protococcus viridis* Ag. was collected. In the water of Lake Waiau, altitude 13,007 feet, diatoms and *Scenedesmus* were collected with a dredging net. On the margins of Lake Waiau, es-

pecially on the north side, masses of fila-
mentous green-colored algae, including
microscopic forms, were submerged and
floating in shallow water (fig. 21).
These have been identified as follows:
*Anabaena* sp., *Aphanothece pallida*
(Kütz.) Rabenh., *Oscillatoria animalis*
Ag., *O. formosa* Bory, *O. irrigua* Kütz.,
diatoms, *Cosmarium* sp., *Haematococcus
pluvialis* Flotow em. Wille, *Ulothrix
subtilissima* Rabenh., *Scenedesmus*. The
names preceded by an asterisk are addi-
tions to MacCaughey's list of Hawaiian
algae ('18).

Mosses collected on the Expedition
were determined by E. B. Bartram.
They include 36 species and varieties, 23
(64%) of which are endemic, 9 (25%)
cosmopolitan or widespread, 3 (8%)
from eastern Asia and islands of the
Pacific, and 1 (3%) from Europe. They
comprise 26 genera and 14 families.
Among them are 3 new species: *Brachy-
thecium hawaiicum*, *Anoectangium hartt-
iae*, and *Mielichhoferia nealiae*.

*Brachythecium hawaiicum*, found on
the trunk of an introduced tree, *Cupressus
macrocarpa*, at Humuula (altitude 6,700
feet), belongs to a widespread genus of
about 190 species, which live mostly in
temperate regions in America and Asia,
on many kinds of substrata. *Anoectan-
gium harttiae*, collected at Laumaia (alti-
tude 6,570 feet) in a dry, rocky stream
bed, also belongs to a widespread genus
of about 45 species, which live chiefly in
temperate regions in Africa, Asia, and
America, on rocks, seldom on the ground.
*Mielichhoferia nealiae*, collected above
Laumaia (altitude 9,500 feet), near the
timberline, belongs to a widespread genus
of about 60 species, 44 of which live in
America, chiefly in mountains on rocks
and ground.

One cosmopolitan species of mosses,
*Bryum capillare*, was collected for the
first time in the Hawaiian Islands. An-
other cosmopolitan species, *Polytrichum
piliferum*, and a European variety, *Tor-
tula alpina* var. *inermis*, were collected for
the first time since 1874. For such low

plant forms, with spores easily carried by
air currents, one would expect to find a
much larger number of cosmopolitan
species in Hawaii. Their high endemism
suggests an origin clouded in as much
mystery as that of the higher plants. One
of these mosses, *Bryum capillare*, was col-
lected at an altitude of 12,350 feet, where
it was hanging in gray fringes from the
rocky ceiling of a small cave at an ancient
Hawaiian adz quarry. This cosmopolitan
genus includes 625 species, which live on
ground and rocks, seldom on trees. *Poly-
trichum piliferum* was collected in two
places at altitudes of 6,200 and 6,400 feet,
just east of Humuula, one specimen on
pahoehoe, one in pasture land. The
genus *Polytrichum* includes 106 species,
most living in America and Africa, grow-
ing on dry or damp earth, in swampy
spots, and on rocks. *P. piliferum* has
been found on sandy, rocky, dry places
from lowlands to high mountains through-
out Europe, covering large areas, also in
northern Asia, Japan, North and South
America. *Tortula alpina* var. *inermis*
was collected in three places: on the trunk
of a juvenile *Cupressus macrocarpa* grow-
ing beside the house at the Humuula
Sheep Station (altitude 6,700 feet); on
rough lava by the trail above Humuula
(altitude 8,250 feet); on the trunk of a
*Sophora* tree or on a rock beneath, near
Hookomo (altitude 7,800 feet). The
genus *Tortula* includes about 186 species
and is widespread, being best represented
in America and Africa. Strangely, the
variety has been recorded previously only
from Switzerland, northern Italy, and
the Tyrolean Alps, where it grows on
shaded rocks, never on wood. Concern-
ing this variety, Bartram ('39) says:
"The only explanation I can find [for
its presence in Hawaii] is that typical
*T. alpina* seems to have a wide range
in alpine regions from Europe to eastern
China, so that the original source of the
Hawaiian plant may have been in Asia."

Four species of mosses and one variety
previously found on other islands of the
Hawaiian group were collected on the

island of Hawaii for the first time. Four more species were collected for the first time since 1874.

The commonest moss seen during the Expedition, *Rhacomitrium lanuginosum* var. *pruinosum*, belongs to the Grimmiaceae, a family spread over the whole earth, most species being in the subarctic and temperate zones. The genus also is widespread and includes about 88 species, the greatest number of which are in America and Africa, growing chiefly on rocks. This variety is found in Hawaii, New Zealand, Tasmania, and Africa. On Mauna Kea it was found forming dense hoary mats on lava flows below Humuula, and it was seen at altitudes between 6,200 and 11,500 feet. Bartram states ('33) : " The Hawaiian plants are all referable to the austral variety *pruinosum*, which is distinguished from the typical form of the Northern Hemisphere by the longer hyaline points with more coarsely spinulose-dentate margins. It is common in exposed, barren places at high elevations, especially in the vicinity of Kilauea, Hawaii. The collections from Mauna Loa (13,680 feet) by Mr. Brummagin probably represent the highest elevation known for any insular moss in the world." This moss has also been collected at 8,000 feet on the summit of Hualalai, Hawaii, at a similar altitude in the crater of Haleakala, Maui, and in bogs of Molokai and Kauai. The highest moss collected by the Expedition was an endemic species, *Grimmia haleakalae*, at 13,350 feet, in rock crevices. It had been collected previously on Mauna Kea, Mauna Loa, Hualalai, and Haleakala, but not higher than 9,700 feet.

The list of mosses, included in the List of Plants, has been compared with citations by Brotherus ('27) and Bartram ('33, '39) and also with a list of specimens in the Bishop Museum collected in 1874 by Sven Berggren of Sweden. Brotherus and Bartram examined specimens found by more than ten botanists who had made the most thorough and valuable collections of Hawaiian mosses.

The ferns include 20 species: 10 (50%) endemic, 6 (30%) cosmopolitan or widespread, 2 (10%) from Asia or Fiji, and 2 (10%) from America. They are included in 12 genera and 2 families.

The spermatophytes include 90 species and varieties: 46 (51%) endemic, 9 (10%) cosmopolitan or widespread, 7 (8%) from Australia and islands of the Pacific, 7 (8%) from America, 15 (17%) from Europe, 6 (6%) from Eurasia and Africa. They are included in 68 genera and 39 families.

The grass family has the largest number of species, 14, 5 of which are endemic, 6 from Europe, 1 from Australia, 1 from Australia and New Zealand, 1 from Eurasia and Africa. The dominant grasses on the plain between Mauna Kea, Mauna Loa, and Hualalai, according to Hitchcock ('22), are *Eragrostis atropioides* and *E. leptophylla*, growing in tufts over large areas. Hitchcock says: " Toward the upper limit of vegetation on the high mountains of Hawaii, above timberline and extending down into the upper open forest are three common species of grasses, *Trisetum glomeratum*, *Agrostis sandwicensis*, and *Aira* (*Deschampsia*) *nubigena*."

The composite family has the second largest number of species, 13, 5 of which are endemic, 3 from Europe, 4 widespread, 1 from America. The other families are more meagerly represented, the third largest number being the legumes with 6 species, 2 endemic; and the fourth largest number the pinks with 5 species, 1 endemic.

LIST OF PLANTS

MUSCI

*Amphidium cyathicarpum* (Mont.) Broth. (C).[3] Maui (east), 4,000–8,500 (EB) ; [4]

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[3] Distribution: (Af), Africa; (Am), America; (As), Asia; (Au), Australia; (C), widespread; (E), endemic; (Eu), Europe; (NZ), New Zealand; and (P), east Asia and Pacific islands.

[4] Distribution in the Hawaiian Islands, as collected or cited by (SB), Sven Berggren; (VB), V. F. Brotherus; (EB), E. B. Bartram; and (HN), Hartt and Neal. Altitude in feet.

Hawaii, Mauna Kea, Argyroxiphium region (SB) ; Hawaii, Laumaia, 6,570 (HN).

*Anoectangium haleakalae* (C. M.) Par. (E). Maui (east), 6,000–6,500 (EB) ; Hawaii, east of Humuula, 6,200 (HN).

*Anoectangium harttiae* Bartr., n. sp. (E). Hawaii, Laumaia, 6,570 (HN).

*Brachythecium hawaiicum* Bartr., n. sp. (E). Hawaii, Humuula, 6,700 (HN).

*Brachythecium lamprocarpum* (C. M.) Jaeg. (P). Maui (east) ; Hawaii, Bird Park, Kilauea, Hualalai; 3,600–6,500+ (EB) ; Hawaii, Mauna Kea, 6,500 (SB) ; Hawaii, Humuula and Puu Huluhulu, 6,600–6,700 (HN).

*Brotherella opaeodon* (Sull.) Broth. (E). Maui (west) ; Kauai; 3,600–4,800 (VB) ; Kauai; Oahu; Maui (east and west) ; Hawaii, east base of Mauna Kea, 4,000–6,000 (EB) ; Hawaii, Laumaia, 5,800 (HN).

*Bryum capillare* L. (C). Hawaii, Mauna Kea, adz quarry, 12,350 (HN).

*Campylopus hawaiico-flexuosus* (C. M.) Par. (E). Oahu; Kauai; Maui (east and west) ; 600–6,000 (EB) ; Hawaii, Mauna Kea (SB) ; Hawaii, Laumaia, 5,800 (HN).

*Campylopus introflexus* (Hedw.) Brid. (C). Kauai; Hawaii, Kilauea, Hualalai; 4,000+ (EB) ; Hawaii, Mauna Kea, 6,500 (SB) ; Hawaii, Humuula, at Puu Huluhulu, 6,600 (HN).

*Campylopus purpureo-flavescens* Hpe. (E). Kauai; Hawaii, Hilo; 500±–3,600 (VB) ; Oahu; Molokai; Maui (east) ; 2,000–4,000 (EB) ; Hawaii, east of Humuula, 6,200 (HN).

*Ceratodon purpureus* Brid. (C). Maui (west) ; Hawaii, Hualalai, Bird Park, Mauna Loa; 3,300–10,000 (VB) ; Maui (east) ; Hawaii, Kilauea, Kipuka Nene, Hualalai; 4,000–9,000 (EB) ; Hawaii, above Humuula, Mauna Kea-Humuula Trail, Laumaia, 7,600–9,500 (HN).

*Dicranum speirophyllum* Mont. (E). Oahu, 1,500 (VB) ; Kauai; Maui (east and west) ; Oahu; Hawaii, Kilauea, Hualalai, Papaloa; 1,000±–8,000 (EB) ; Hawaii, Mauna Kea (SB) ; Hawaii, east of Humuula, 6,200 (HN).

*Dicranum speirophyllum* var. *breviflagellare* (C. M.) Bartr. (E). Oahu; Maui (east) ; 2,500–4,000 (EB) ; Hawaii, Humuula at base of Puu Huluhulu, 6,600 (HN).

*Encalypta sandwicensis* Sull. (E). Hawaiian Islands (Wilkes Expedition, 1859) ; Hawaii, Mauna Kea, Sophora region (SB) ; Hawaii, above Hookomo, 7,800 (HN).

*Grimmia haleakalae* Rchdt. (E). Hawaii, Mauna Loa, Rest House; Hualalai, near top; Maui (east) ; 6,000–10,000 (VB) ; Maui (east), 6,000–9,700 (EB) ; Hawaii, Mauna Kea, Argyroxiphium region (SB) ; Hawaii,

Mauna Kea, east slope, 9,000 (Skottsberg) ; Hawaii, near Hookomo, near summit of Mauna Kea, 7,600–13,350 (HN).

*Grimmia trichophylla* Grev. (C). Maui (east) ; Hawaii, top of Hualalai, 6,000–9,700 (EB) ; Hawaii, above Humuula, 7,600–8,250 (HN).

*Isopterygium albescens* (Schwaegr.) Jaeg. (P). Oahu; Molokai; Hawaii, Kilauea, Makaopuhi, 500–4,000 (EB) ; Hawaii, Laumaia, 5,800 (HN).

*Isopterygium vineale* Bartr. (E). Maui (east), near Olinda, Ukulele; Maui (west) ; Molokai; Kauai, 4,000–6,000 (EB) ; Hawaii, Laumaia, 5,800 (HN).

*Leptobryum pyriforme* (Hedw.) Wils. (C). Hawaii, Kilauea, 3,600 (Skottsberg) ; Hawaii, Hookomo, 7,500 (HN).

*Leptodontium brevicaule* Bartr. (E). Hawaii, Kilauea, Bird Park, 3,600–4,200 (EB) ; Hawaii, Mauna Kea (SB) ; Hawaii, near Humuula, 6,200–6,600 (HN).

*Macromitrium intricatum* C. M. (E). Maui (east), 7,200 (VB) ; Maui (east and west) ; Oahu; 1,000–8,000 (EB) ; Hawaii, Mauna Kea, 6,500 (SB) ; Hawaii, Humuula at Puu Huluhulu, 6,600 (HN).

*Mielichhoferia nealiae* Bartr., n. sp. (E). Hawaii, Laumaia, 9,500 (HN).

*Mielichhoferia pulvinata* C. M. (E). Maui (east), Puu Nianiau, 6,500 (EB) ; Hawaii, Laumaia, Mauna Kea at foot of highest peak, 6,570–13,100 (HN).

*Orthotrichum hawaiicum* C. M. (E). Maui (east), 7,200 (VB) ; Maui (east) ; Hawaii, Laumaia, above Kukaiau Ranch, 6,570–9,000 (EB) ; Hawaii, Humuula, above Hookomo, 6,700–7,800 (HN).

*Orthotrichum hillebrandii* C. M. (E). Maui (east) ; Hawaii, Laumaia, above Kukaiau Ranch, 6,570–9,300 (EB) ; Hawaii, above Hookomo, 7,800–8,000 (HN).

*Philonotis turneriana* (Schwaegr.) Mitt. (P). Kauai, Hanapepe-Wahiawa; Hawaii, Hilo (VB) ; Molokai; Oahu; Kauai, Hanakapiai; Maui (east and west) ; Lanai; Hawaii, Kohala Mts., above Pahala, southwest slope of Hualalai, Kilauea near Makaopuhi; 500?–6,500 (EB) ; Hawaii, Laumaia, 6,570 (HN).

*Pleuropus wilkesianus* (Sull.) Broth. (E). Hawaiian Islands; Oahu (east and west) ; Maui (east and west) ; Kauai; Hawaii, Hualalai; 1,350–7,500 (VB) ; Lanai; Oahu; Molokai; Kauai; Maui (east) ; Hawaii, Manuka, southwest slope and top of Hualalai, Hilo, Mauna Kea; 1,000–8,275 (EB) ; Hawaii, east of Humuula, 6,200 (HN).

*Pleuropus wilkesianus* var. *sciuroides* (C. M.) Bartr. (E). Maui (east) ; Oahu (west) ; 2,000–2,700 (VB) ; Oahu; Kauai; Hawaii, Puuwaawaa; 2,000–4,000 (EB) ; Hawaii,

Humuula at Puu Huluhulu and east, 6,200–6,600 (HN).

*Pogonatum baldwinii* (C. M.) Par. (E). Oahu (east); Maui (east); Hawaii, Mauna Loa, 2,000?–9,000? (VB); Oahu; Maui (east and west); Molokai; Kauai; Hawaii, Kilauea, Pahala, Kohala Mts., Waipio, 500–6,000 (EB); Hawaii, Laumaia, 5,800 (HN).

*Polytrichum piliferum* Schreb. (C). Hawaii, Mauna Kea (SB); Hawaii, east of Humuula, 6,200–6,400 (HN).

*Ptychomitrium mauiense* Broth. (E). Maui (east), 7,200 (VB); Maui (east), 8,000 (EB); Hawaii, Humuula at Puu Huluhulu and east, 6,400–6,600 (HN).

*Rhacomitrium lanuginosum* var. *pruinosum* Hook. and Wils. (C). Maui (east and west); Molokai; Kauai, Alakai Swamp; Hawaii, Kilauea Crater, Kilauea Iki, Mauna Loa, Hualalai; 3,000–13,600 (EB); Hawaii, Humuula at Puu Huluhulu and east, near Hookomo and above, 6,200–11,500 (HN).

*Rhizogonium spiniforme* (L.) Bruch. (C). Molokai; Oahu; Kauai; Maui (east); Hawaii, Hilo, Mauna Loa, Kilauea, Haena, Hiulani (near Olaa); 720–4,200 (VB); Molokai; Oahu; Kauai; Maui (east and west); Hawaii, Kilauea, Kilauea Iki, near Olaa, Mauna Loa; 600–6,000 (EB); Hawaii, Laumaia, 5,800 (HN).

*Thuidium plicatum* Mitt. (E). Molokai; Oahu; Kauai; Maui (east); Hawaii, Kilauea; 2,800–6,000 (EB); Hawaii, Mauna Kea (SB); Hawaii, Laumaia, Humuula, 5,800–6,700 (HN).

*Tortula alpina* var. *inermis* (Milde) DeNot. (Eu). Hawaii, Mauna Kea, Argyroxiphium region (SB); Hawaii, Humuula and above Hookomo, 6,700–8,250 (HN).

*Weisia ovalis* (R. S. W.) Bartr. (E). Molokai; Oahu; Kauai; Maui (west); Lanai; Hawaii, Kohala, Kilauea; near sea level to 4,000 (EB); Hawaii, Hookomo, 7,500 (HN).

## FILICES

*Asplenium adiantum nigrum* L. (C). 500–13,000 [5] (6,400–13,500)
*Asplenium nitidulum* Hbd. (E). 2,000–3,600 (5,800)
*Asplenium rhomboideum* Brack. (E). 4,000–9,300 (6,200–9,600)
*Asplenium trichomanes* L. (C). 1,600–12,500 (6,400–10,000)
*Athyrium poiretianum* (Gaud.) Presl (E). 1,000–6,300 (5,800–6,400)
*Cibotium chamissoi* Kaulf. (E). 1,000–4,300 (6,700)
*Diplazium sandwichianum* (Presl) Diels (E). 1,000–6,500 (5,800)
*Dryopteris glabra* (Brack.) O. Ktze. (E). 1,000–6,700 (5,800)
*Dryopteris hawaiiensis* (Hbd.) Rob. (E). 4,000–5,000 (5,800)
*Dryopteris paleacea* (Swz.) C. Chr. (Am). 3,000–11,500 (5,800–9,600)
*Elaphoglossum conforme* (Swz.) Schott (E). 3,500–8,000 (5,800)
*Elaphoglossum hirtum* (Swz.) C. Chr. (C). 1,500–8,000 (5,800–6,400)
*Hypolepis punctata* (Thunb.) Mett. (C). 3,000–6,000 (5,800)
*Pellaea ternifolia* (Cav.) Link (Am). 1,950–9,800 (6,400–10,400)
*Polypodium hookeri* Brack. (P). 2,000–7,000 (6,200)
*Polypodium lineare* Thunb. (As). 700–6,000 (6,800)
*Polypodium pellucidum* Kaulf. (E). 750–9,500 (5,800)
*Pteridium aquilinum* (L.) Kuhn (C). 500–8,250 (6,600–9,600)
*Pteris cretica* L. (C). 2,700–7,000 (6,200)
*Sadleria cyatheoides* Kaulf. (E). 100–4,000 (6,600)

## SPERMATOPHYTA

*Acacia koa* var. *hawaiiensis* Rock (E). 3,000–6,000 (5,800–7,000)
*Achillea millefolium* L. (C). 3,000–6,000 (6,800)
*Agrostis retrofracta* Willd. (Au). 2,000–8,250 (6,200–9,500)
*Agrostis sandwicensis* Hbd. (E). 3,600–13,000 (9,500–13,100)
*Anthoxanthum odoratum* L. (Eu, Af, As). 2,500–7,000 (6,700–13,007)
*Arenaria leptoclados* Reichenb. (Eu). —— (7,800)
*Arenaria serpyllifolia* L. (Eu, As). —— (7,000)
*Argyroxiphium sandwicense* DC. (E). 6,000–12,000 (10,500 [dead], 12,250 [living + dead])
*Astelia menziesiana* Smith (E). 2,700–4,000 (5,800)
*Bromus mollis* L. (Eu). 1,000–7,500 (7,000)
*Carex sandwicensis* Boeck. (E). 1,000–9,000 (6,200)
*Carex wahuensis* C. A. Mey. (E). 1,700–7,000 (6,600)

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[5] Altitudinal range, in feet, in Hawaiian Islands. Collections by Hartt and Neal are given in parentheses.

*Centaurium umbellatum* Gilib.  (Eu).  200–6,000  (7,000)
*Cerastium vulgatum* L.  (Eu).  1,000–13,007  (6,800–13,007)
*Cheirodendron gaudichaudii* (DC.) Seem.  (E).  1,500–6,000  (5,800)
*Chenopodium ambrosioides* L.  (Am).  15–8,000  (6,000–7,000)
*Chenopodium oahuense* (Mey.) Aell.  (E).  10–7,000  (6,000–8,250)
*Cirsium vulgare* (Savi) Airy-Shaw  (Eu).  2,000–6,800  (5,000–13,007)
*Coprosma ernodeoides* var. *typica* St. John (E).  1,500–10,000  (6,400–9,600)
*Coprosma ernodeoides* intermediate to var. *mauiensis*  (E).  6,000  (6,200)
*Coprosma montana* var. *typica* Oliver (E).  3,000–10,500  (6,700–8,250)
*Coprosma rhynchocarpa* Gray?  (E).  2,000–6,000  (5,800)
*Cupressus macrocarpa* Hartw.  (Am).  3,600–3,900  (6,700)
*Danthonia pilosa* R. Br.  (Au, NZ).  3,000–7,000  (7,000)
*Deschampsia nubigena* Hbd.  (E).  3,000–9,300  (6,300–7,500)
*Dodonaea viscosa* L.  (C).  700–8,250  (6,500)
*Dubautia arborea* (Gray) Keck  (E).  5,000–10,000  (8,250)
*Dubautia ciliolata* var. *juniperoides* (Gray) Keck  (E).  3,500–10,500  (8,750–10,300)
*Epilobium oligodontum* Haussk.  (Japan).  4,500–7,000  (6,700–6,800)
*Eragrostis leptophylla* Hitchc.  (E).  4,000–6,000  (6,400–7,000)
*Erigeron linifolius* Willd.  (C).  100–4,000  (7,800–13,007)
*Erodium cicutarium* (L.) L'Hérit.  (Eu).  500–7,000  (6,800–7,800)
*Euphorbia olowaluana* var. *gracilis* (Rock) Sherff  (E).  2,000–5,000  (6,300)
*Festuca dertonensis* (All.) Aschers. and Graebn.  (Eu).  800–8,500  (6,780)
*Festuca myuros* L.  (Eu).  1,600  (8,000–8,250)
*Geranium carolinianum* var. *australe* (Benth.) Fosb.  (Am).  2,000–6,000  (6,800)
*Geranium cuneatum* var. *hololeucum* Gray (E).  4,000–10,800  (6,400–9,600)
*Geranium multiflorum* var. *typicum* Knuth  (E).  4,000–6,000  (7,226)
*Gnaphalium japonicum* Thunb.  (C).  1,000–8,250  (6,400–9,600)
*Gnaphalium purpureum* L.  (Am).  150–4,000  (6,400–6,800)
*Gnaphalium sandwicensium* Gaud.  (E).  15–8,250  (6,600–10,000)
*Heleocharis obtusa* var. *enotata* Hbd.  (E).  4,000  (6,200)
*Hesperocnide sandwicensis* Wedd.  (E).  2,000–6,000  (8,000)
*Hordeum murinum* L.  (Eu).  1,000–4,000  (7,000–8,000)
*Hydrocotyle verticillata* Thunb.  (C).  500–3,225  (6,200)
*Hypericum japonicum* Thunb.  (As, Au).  4,000–5,000  (5,800)
*Ilex anomala* (H. and A.) Heller  (E).  900–6,000  (5,800)
*Leontodon autumnalis* L.  (Eu).  4,000–6,000  (6,800–9,600)
*Lepidium virginicum* L.  (Am).  15–8,500  (6,800–7,800)
*Luzula hawaiiensis* Buchen.  (E).  2,000–9,300  (6,800–9,600)
*Metrosideros collina* subsp. *polymorpha* Gaud.  (P).  1,200–6,000  (5,800–6,600)
*Metrosideros collina* subsp. *polymorpha* var. *typica* Rock  (E).  1,000–9,000  (6,200)
*Modiola caroliniana* (L.) G. Don  (Am, Af).  2,500–6,000  (6,400–6,800)
*Myoporum sandwicense* Gray  (E).  10–10,000  (6,700)
*Oxalis corniculata* L.  (C).  6–3,600  (6,780–7,800)
*Panicum tenuifolium* Hook. and Arn.  (E).  3,600–7,500  (6,400–7,500)
*Peperomia cookiana* var. *minutilimba* Yuncker  (E).  5,000±  (6,600)
*Peperomia reflexa* var. *parvifolia* C. DC.  (As, P).  500–6,500  (5,800)
*Phytolacca brachystachys* Moq.  (E).  50–6,000  (5,800)
*Pinus contorta* Loudon  (Am).  6,500–13,007  (13,007)
*Plantago pachyphylla* var. *hawaiiensis* Gray  (E).  2,000–8,200  (6,400)
*Plantago virginica* L.  (Am).  2,700–6,000  (6,200)
*Poa annua* L.  (Eu).  200–13,000  (7,800–13,007)
*Poa pratensis* L.  (Eu).  3,600–6,700  (13,007)
*Ranunculus hawaiiensis* Gray  (E).  3,500–9,000  (9,600)
*Rubus hawaiiensis* Gray  (E).  2,000–7,000  (6,200–7,500)
*Rumex acetosella* L.  (Eu, Am).  3,000–7,000  (6,600–13,007)
*Santalum pilgeri* Rock  (E).  2,000–5,200  (8,000)
*Senecio sylvaticus* L.  (Eu).  1,500–7,000  (7,800–10,000)
*Sicyos* sp.  (E).  ——  (6,600)
*Silene struthioloides* Gray  (E).  2,000–9,500  (9,500)
*Sisymbrium officinale* L.  (Eu, Af).  1,800–3,000  (6,700–6,800)
*Sisyrinchium acre* Mann  (E).  3,000–9,300  (6,400–9,000)
*Solanum nigrum* L.  (C).  10–5,000  (7,800)

*Sophora chrysophylla* (Salisb.) Seem.   (E).   2,000–10,000   (6,400–9,500)
*Stellaria media* Cyrill.   (Af, As, Eu).   3,000   (13,007)
*Styphelia douglasii* (Gray) F. Muell.   (E).   4,000–10,800   (6,400–10,500)
*Styphelia tameiameiae* (Cham.) F. Muell.   (E).   900–9,500·+   (8,500)
*Suttonia lessertiana* (A. DC.) Mez   (E).   1,500–6,000   (5,800)
*Taraxacum officinale* Weber   (C).   2,000–13,007   (6,800–13,007)
*Tetramolopium humile* var. *skottsbergii* Sherff   (E).   6,000–10,000   (6,400–10,000)
*Trifolium arvense* L.   (Af, As, Eu).   7,000–9,000   (6,800–7,800)
*Trifolium dubium* Sibith.   (Eu).   4,000–6,000   (6,800)
*Trifolium repens* L.   (As, Eu).   4,000–7,000   (6,800–7,800)
*Trisetum glomeratum* (Kunth) Trin.   (E).   1,000–13,000   (8,500–13,400)
*Ulex europeus* L.   (Eu).   6,000   (6,800)
*Vaccinium calycinum* Smith   (E).   1,600–6,000   (6,000)
*Vaccinium peleanum* Skottsb.   (E).   4,000–10,800   (8,500–12,250)
*Vaccinium reticulatum* Smith (E).   1,000–9,500   (6,400–6,570)
*Veronica plebeia* R. Br.   (Au).   3,000–8,250   (7,226)

## SUMMARY.

This paper gives an account of the ecological and floristic features of the vegetation of the summit area of Mauna Kea. The ecological section deals with the climatic, edaphic, and biotic factors of the environment, the zonation of vegetation, and plant succession. The floristic section lists the species of mosses, ferns, and flowering plants, with their altitudinal range in Hawaii and distribution throughout the world.

We are led to conclude that the origin of the vegetation of the summit region of Mauna Kea is from the lower slopes of the mountain.

## ACKNOWLEDGMENT.

We are indebted to the Hawaiian Academy of Science and the United States Army for the management of the Expedition. To the Parker Ranch we owe many thanks for permission to make our headquarters at the Humuula Sheep Station, to study the vegetation on the ranch property, and to make collections of plants. We wish to express thanks to the other members of the Expedition who made valuable additions of specimens. To many individuals we are grateful for aid in determining certain specimens or for suggestions about the manuscript: E. B. Bartram, E. L. Caum, H. E. Gregory, E. Y. Hosaka, H. L. Lyon, J. T. Koster, C. Skottsberg, C. K. Wentworth, and L. D. Whitney.   We are indebted to C. W.

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# REVIEWS

## NOTICE CONCERNING BOOK REVIEWS

The Editors of Ecology would like to have this journal review the important books in the ecological field. To facilitate this it is suggested that (1) publishers send their books directly to either editorial office (Zoölogical books to Thomas Park, The University of Chicago; Botanical books to Francis Ramaley, The University of Colorado), and (2) readers call the

Editors' attention to books they consider significant. For obvious reasons the final decision as to whether a review is acceptable must rest with the Editors. It is felt that if the above suggestions are followed the journal will be able to notice the more important and interesting volumes as they appear.

Editors of Ecology

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## Bio-Ecology [1]

This book, as remarkable for its virtues as for its defects, may be taken as giving a definitive statement of the ecological doctrines of its distinguished authors. The work opens with a brief history of the concept of biological communities, and proceeds in the second chapter to the introduction of the biome or biotic formation as a major ecological unit. A biome is characterized as any one of "the great landscape types of vegetation with their accompanying animals" such as grassland, tundra, desert, coniferous forest, deciduous forest and the like. Actually, the concept of the biome as applied in the later part of the book is more restricted, as several desert, deciduous and coniferous forest biomes are recognized on the North American continent. The biomes are taken to include not only climax communities but all successional stages within their ranges. Subdivisions of both climax and seral stages, following Clements' well-known scheme, are introduced later; the climax subdivisions (association, faciation, etc.) are taken to be differentiations of the biomes and the latter are the products of "climatic differentiation operating on an original community of vast extent and fairly uniform composition." The

[1] Clements, F. E., and V. E. Shelford. 1939. Bio-Ecology. John Wiley and Sons, New York. vi + 425. 85 figs. $4.50.

evidence for this, by no means universally acceptable, view is not critically discussed.

Five chapters are devoted to general aspects of ecology, particularly the reaction of organisms on their habitat, their coactions among themselves, aggregation, competition, migration, and the phenomena of succession. These chapters are replete with valuable information, summarizing a great quantity of work by many investigators; they will be useful to all students of ecology. The general principles that are supposed to emerge are, however, mainly classificatory; processes occur in different communities that can be placed in a single category and designated by a single term. The general principles of ecology therefore appear as a set of rules for the construction of a language. This may be inevitable in the present state of the science; it is, however, uncertain that the language of Bio-ecology will ever become a universal ecological tongue. Its descriptive powers are amply demonstrated in the chapter on the American grassland. In dealing with competition and biological populations, the largely alternative language of mathematics is neglected, the authors having "grave doubt that the statistical approach is applicable to such an intricate complex of causes and effects." They do not, however, provide

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a more delicate and powerful means of investigation.

Some of the material introduced into the middle chapters seems to be treated uncritically. There is, for example, a long discussion on the supposed relationship between solar and biological cycles. The authors accept the thesis that "the solar cycle alone seems capable of bringing order out of the confusion and of assigning proper values to the primary and secondary causes concerned." An impartial review of the most critical work on this subject will, however, indicate that only in the case of tree-ring cycles has any dependence on solar cycles been clearly demonstrated; even here the problem becomes extremely complex when its astrophysical aspects are properly taken into account.

The last three chapters are devoted to the North American grassland, to aquatic climaxes in fresh-waters and to marine biotic communities. The first of these is excellent; it is greatly to be regretted that no detailed treatment of the other terrestrial biomes was possible. The chapter on fresh-water climaxes is quite inadequate. Much interesting information is given, but the fundamental limnological problems involved are never reached. The treatment of marine communities is more thorough, but suffers from a grave theoretical defect.

As a presentation of one aspect of ecology, it will be seen that the scope and detail of the present work make it a valuable contribution, though its value is marred by a somewhat infelicitous style of writing. The gravest defect of the book, in the reviewer's opinion, lies in its total neglect of certain very important approaches to the subject, in which its technical language is of no assistance. If, as is insisted, the community is an organism, it should be possible to study the metabolism of that organism. The neglect of this aspect of ecology, and of the fact that the living matter of the whole earth may be considered as a unit of higher order than the biome, leads the authors to make the following extraordinary statement, "from the very nature of the medium, the reactions of plants upon the air are usually less definite and controlling than upon the soil." Photosynthesis is discussed briefly on the next page, but no idea of the fact, apparent to Joseph Priestley on the conclusion of his experiments, is given that here we are in the presence of the greatest controlling reaction of them all. This neglect of the biogeochemical approach is due in part to the authors' insistence that the community and the environment must be separated and should not be considered as forming part of the same ecological unit. The very interesting work of Schröder, Noddack and others, that suggests a quantitative characterization of major vegetation types in terms of their photosynthetic efficiency, and that permits an estimate of the carbon metabolism of the earth, is completely neglected. The same fundamental attitude leads to a dissociation of the pelagic and benthonic communities in the sea as separate biomes, in the open ocean indeed three pelagic and a benthonic biome, one above the other, are recognised. Only the upper part of this system is trophogenic and the whole assemblage appears to the reviewer as comparable to the layers in a forest and its substratum of soil. There is a bibliography of about nine hundred titles, the majority in English, a brief appendix on field methods, and a good index.

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## A Naturalist in the Hebrides [1]

The chapter headings partially tell the story of this set of essays by the author of *A Herd of Red Deer* and *Bird Flocks and the Breeding Cycle*. They are: "The vivid frontier"; "The display of birds; North Rona"; "The social life of animals"; "Ron mor, the great seal"; "Sanctuaries for wild life"; "The mystery of antlers," and "Forest and island." The book is in the manner of the best modern natural history, which is reviving in England and America the great tradition of the earlier naturalists after that tradition was becoming overcast by triviality and sentimentality. Everywhere Mr. Darling shows a sense of proper restraint: in sentiment, in humanizing interpretations, and even in scientific attitudes.

Except for his study of the Atlantic Gray Seal and for some observations on birds, this book does not break new ground; it tends to consolidate fields on which the author has reported at greater length in his earlier writing. The discussion of antlers seems extraneous to the general unity of the collection. The essay on social life, which summarizes much in Mr. Darling's previous books, as well as matter presented in detail in some of these essays, will be the focus of interest to many biologists. This is based on the idea that the two great natural principles of struggle for existence and of co-operation are not wholly in opposition, but may each have reacted on the other in determining the trend of animal evolution. This present reviewer finds the concept increasingly more stimulating and convincing.

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## Fossil Nothofagus Pollen [1]

All too few are the efforts of investigators to identify the species of fossil pollens represented in the deposits of their studies. The few attempts which have been made to distinguish the species of *Betula, Pinus*, etc., reveal that in most cases statistical methods are required; first in the study of modern pollens, then in the study of fossil grains. Laborious though such methods may be, they are warranted by the more exact climatic and ecologic interpretations which can be made from specific determinations, rather than those only of the genus.

It is with pleasure and stimulation that one reads Miss Cranwell's first of a series of detailed studies leading toward an atlas of pollen types in the New Zealand flora,

which she had promised in an earlier paper.[2]

She attempts a separation of the species of *Nothofagus* because of their importance as indicators of forest and climate change; because the pollens of the species are well, widely, and sometimes abundantly preserved; and because of the problems of modern, Tertiary and Pleistocene distributions of Fagaceae in both hemispheres. The reported Tertiary occurrence of *Fagus* in New Zealand and Australia, as based on leaves, should be verified by pollen studies since the two genera are readily distinguished. *Nothofagus* grains do not have the tricolpate structure of *Fagus*, but usually have 6–8 (4–10) equatorially arranged pores and a discoid grain.

Her statistical studies revealed characteristic grain-size ranges and pore-frequency curves for the species of *Notho-*

[1] Darling, F. Fraser. 1939. A Naturalist on Rona, Essays of a Biologist in Isolation. *Oxford University Press.* 137 pp., 37 Pl., Map of North Rona. Price $2.50.

[1] Cranwell, L. M. 1939. Southern-beech pollens. *Rec. Auckland Inst. Mus.* 2: 175–196.

[2] Cranwell, L. M. 1938. Fossil pollens. *New Zealand Jour. Sci. Tech.* 19: 628–645.

*fagus.* For example, *N. fusca* has a diameter of 34–42 μ and about 70 per cent of the grains with 8 pores; *N. Menziesii* a diameter of 40–65 μ and about 75 per cent with 7 pores; *N. truncata* a diameter of 23–32 μ and about 55 per cent with 6

pores and 45 per cent with 7 pores. One hundred grains of each species proved to be an abundance for statistical studies.

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## THE VEGETATION OF THE EASTERN ALPS [1]

The Alps, Europe's largest and best-known mountain range, are customarily divided by a line running approximately in a north-south direction from Lake Constance by way of the Rhine Valley to Lake Como. Of these, the Eastern Alps correspond roughly in area to the former Austria but with the Danube as the northern and the Po as the southern limit. They differ from the Western Alps in more than one respect, notably in their geologic, physiographic, and climatological characteristics.

Nowhere in Europe does it seem possible to find a more manifest illustration of the dependence of vegetation upon climate and physiography of the region than in the Alps. Although a favorite collecting ground for some time past, no one had as yet attempted to present the vegetation of the Eastern Alps as a whole.

The author plunges *in medias res* by referring the reader to available sources on the geology and geography of the region and by clearly delimiting his area to the West by means of the so-called "Tessinian Gap" resulting from the peculiar distribution of certain plant species. In contrast to the attempts of others to divide the Eastern Alps into provinces, etc., on the basis of floristic or climatological analyses (Engler, Hayek, Gams, et al.), Scharfetter bases his classification upon the vegetation itself (see map p. 19):

1. The marginal deciduous forest zone.

    (a) Northern and eastern sections.

(b) Southern section.

2. The outer mixed forest zone.
3. The inner coniferous forest zone.

Like all such attempts, this classification has its difficulties. Although admittedly horizontal in orientation, each of these zones is divided into various superseding belts of vegetation. The entire system is shown on the appended map, the last one of its kind published.

The richness and composite character of the vegetation is due to the fact that five major floras, the Mediterranean, Illyrian, Pannonian, Baltic, and Alpine floras contribute certain elements. In separate chapters each of these floras receives detailed study by listing its general characters, key species, floral history, and principal plant communities, both natural and man-made. To what degree the description of the latter, for example, has proceeded can be seen from the sociological classification of meadow types according to Rübel (1933) reproduced on p. 208, or the list of alpine meadows of the Grossglockner on p. 263. As far as possible, the communities are designated and grouped in the manner used by plant sociologists, *e.g.,* Pinetum silvestris astragalosum, Curvuletum, Salicion herbaceae, and Rhodoretalia. Although species lists and details of particular stands had to be omitted, the salient features of all known vegetation types are recorded and properly integrated.

The last chapter records the history of the plant life of the Eastern Alps from the orogeny of the Alps to historic times (the account of the latter was contributed by Hans Pirchegger). The oldest known

fossils, paleophytic and mesophytic re-
mains are excluded, date from the Upper
Cretaceous and are at present either en-
tirely tropical (*Pandanus*) or at least ex-
tra-European (*Sequoia, Brasenia*) while
others still occur in the Alps (*Quercus,
Ulmus,* etc.). Rich Tertiary deposits re-
veal a flora of wide distribution, known
as "Arctic Miocene" flora. The author
uses the theory of alternating orogenies
of parts of the Alps to account for the
phenomena of speciation among genera
with large numbers of oreophytic species,
*e.g., Primula, Gentiana, Saxifraga;* for
the pre-glacial origin of many vicarious
species inhabiting the Western and East-
ern Alps, respectively; and for the con-
clusion that the high alpine flora of the
Alps is not uniform in origin, but is de-
rived from at least four different develop-
mental centers. The Glacial Period too
had its lasting effect upon the flora of the
Alps, as in the formation of bicentric
areas (western and eastern), and fre-
quently in consequence of the disruption
of a larger area occupied by an ancestral
and intermediate type by the isolation and
separation of widely differing sibs of the
present flora. Considerable pollen ana-
lytical data for the postglacial period are
available and the migration of the impor-
tant forest trees can be reconstructed

from these with sufficient accuracy to
allow correlation with northern European
series. The pre-historic remains show
that the Alps were inhabited by man be-
fore the glaciers had completely retreated.
They range from the Early Paleolithic to
the beginning of historic times with the
occupation by the Romans in 16 B.C.

Some critical comments by H. Gams
are appended and reveal the existing dis-
agreement concerning certain important
problems. An extensive bibliography is
evidence of the widely scattered literature
and the care with which the author has
summarized it. The book is concluded
with an index to all plant names used.

The absence of illustrations showing
most of the types of vegetation should
not disappoint the reader in view of the
promise of a pictorial companion volume
to be issued in the near future.

The book represents a critical summary
of available information and of the au-
thor's mature views as gained from a life-
long acquaintance with the vegetation of
the Eastern Alps. Ecologists are indebted
to him for his definite and noteworthy
contribution to the knowledge of alpine
vegetation.

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SOIL CONSERVATION [1]

As the author notes in his preface, no
economic problem in the United States is
more urgent today than the conservation
of our soil. It is a problem of our own
creating, for the pioneers who carried our
civilization across the continent from the
Atlantic to the Pacific Coast "exploited
and abused the soil" and created the con-
ditions which favored its erosion by wind
and rain, causing an economic loss which
already is being felt by thousands of

farmers. A circular of the U. S. Depart-
ment of Agriculture, as early as 1928,
designated soil erosion as a "national men-
ace," and in 1933 the Department of the
Interior established a "Soil Erosion Serv-
ice," with an appropriation of $5,000,000
under the National Industrial Recovery
Act (NIRA). The book is therefore
most timely.

Part one (312 pages) deals with "Soil
Erosion," and part two (646 pages) with
"Soil Conservation." The major and
minor problems of erosion and control are
considered in a scholarly way and out of

[1] Bennett, Hugh Hammond. 1939. Soil
conservation. xvii + 993. 358 figs. Mc-
Graw-Hill Book Co., New York. $6.00.

a wide practical experience in the subject, and the matter is thrown into significant perspective by historical treatment going as far back as writings on erosion of 3000 years B.C. in Mesopotamia, "the cradle of European agriculture." Definitely ecological treatment includes chapters on the relation of erosion to crop yields and changes in the native vegetation, the relation of entomology to soil erosion, farm and range plants useful for erosion control and water conservation, wild life and soil conservation, and so on. In fact the entire book is a treatise on applied ecology—plant, animal, and human; with a

chapter on Research, its function in this connection, the problems involved, and the research program of the Soil Conservation Service of the U. S. Department of Agriculture. The many excellent illustrations are uniformly instructive.

The book is a pioneer in the subject dealt with, and will take its place at once as an indispensable work of reference for everyone who is occupied with the problem of soil erosion from the standpoint of field practice or of scientific research and teaching.

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

## APPLIED SILVICULTURE [1]

For many years there has been a definite need for the synthesis of silvicultural literature in order that such information could be utilized as a sound basis for the management of the different forest types of the United States. In some respects this book succeeds in fulfilling this need. This is particularly true in regard to treatment of the forest as a crop; however, some of the other silvicultural aims of management, such as soil erosion and watershed protection, are either neglected or treated only secondarily.

The author has approached the subject of applied silviculture by first classifying and describing the different forest areas. Each forest type is treated first on the basis of its historical background. Then the forest and its management are considered. As a rational basis of management, special emphasis is placed upon the ecological and economic aspects of each of the forests. Where information is available, the author has gone into detail concerning the methods of cutting, cutting operations, planting or regeneration, the various methods of slash treatment,

and other practical aspects of management. While a large portion of the statements are supported by experimental data, in numerous places it is evident that the statements are supported only by general observations. This suggests that much research needs to be done even in the regions most intensively studied.

One of the more valuable features of the book, particularly for the ecologist, is the brief summary, sometimes in tabular form, of the various forest types as to area covered, commercial value, sites occupied, associated species, and place in succession. The most important diseases and insect problems are treated on an ecological basis and suggestions made as to possible practical methods of dealing with them.

This book should prove of particular value as a reference for advanced students of silviculture and those who are actively engaged in forest management. Also, the inclusion of a comprehensive bibliography at the end of each chapter makes this a very good source reference for those interested in silvicultural research.

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[1] Westveld, R. H. 1939. Applied Silviculture in the United States. *John Wiley and Sons, Inc.* New York. 567 pp. $5.00.

## PRELIMINARY ECOLOGICAL SURVEY OF THE ISLAND OF HAWAII [1]

Beginning with a description of the location, area, and mountains involved, the authors then mention the economic importance of ecological studies in Hawaii and review some of the work already done by others. The environmental factors are then discussed. Climatic factors vary more than edaphic, the greatest variable being rainfall. There is considerable variation in both rainfall and temperature for different areas, but little seasonal variation. Sunshine, soil origin, weathering, soil fertility, and water-holding capacity are all discussed.

The climax formations are: I. Forests; Coastal-lowland forest (hygrophytic), Transition forest (xerophytic) and Mountain forest (mesophytic). II. Parklands; Plateau parkland (xerophytic) and Mountain parkland (xerophytic). III. Shrubs; Coastal-lowland shrub and Subalpine shrub (both xerophytic). IV. Alpine moss-lichen formation (xerophytic). V. Mountain bog formation (hygrophytic). These formations are compared with those of Hillebrand and Rock, are delimited altitudinally, and are presented in an excellent map.

The most prominent associations in the coastal-lowland forest are those of *Pandanus-Cocos* and *Aleurites-Pandanus*. The transition forest has no dominant species; some characteristic genera are *Straussia, Suttonia, Sapindus, Pelea, Sophora, Metrosideros, Antidesma,* and *Nototrichium*. The characteristic association of the mountain forest is that of *Metrosideros-Cibotium*. In the plateau parkland the *Myoporum-Sophora* association is widespread. *Acacia Koa, Sophora* and *Metrosideros* are the chief trees in the mountain parkland. The coastal-lowland shrub is now mainly given over to introduced plants; *Maba sandwicensis* is the most typical native shrub. Typical associations in the subalpine shrub are

those of *Dodonaea-Styphelia* and *Styphelia-Coprosma*. The most abundant plant in the alpine moss-lichen formation is *Rhacomitrium lanuginosum* var. *pruinosum*. Common plants in the bog formation include *Lycopodium* spp., *Selaginella deflexa, Schizaea-robusta,* and *Suttonia sandwicensis*. This classification of formations seems in the main to be workable. The reviewer desires to call attention to other work on zonation of Mauna Kea presented in this same issue.

An ecologist like Dr. Robyns would of course be impressed by the importance of studies of plant succession on the dated lava flows of Hawaii. The authors present data from the Kilauea region and summarize the progress of invasion as follows: first, the invasion of cracks in new flows by ferns and flowering plants common to the adjacent area, and supported by cryptogams especially on the *aa* flows; second, the gradual building up of a heavier plant covering, filling in between the cracks, producing a shrub stage; and finally, the production of a plant community typical of the formation on the adjacent area.

The island of Hawaii is rapidly losing its indigenous vegetation due to grazing, clearing for agricultural purposes, volcanic action, insect injury, and the introduction and spread of foreign plants. Consequently any study of the present condition of plants on that island is of value. This preliminary ecological survey represents an attempt toward a very difficult and complex subject, and it is to be hoped that since one of the authors is a resident of the island of Hawaii, further more detailed collections will be made particularly of the plants on the dated lava flows and in the *kipukas*.

The report is well illustrated with two maps and many photographs.

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[1] Robyns, W., and S. H. Lamb. 1939. Preliminary ecological survey of the island of Hawaii, *Bull. Jard. Botan. de l'État, Bruxelles* **25**: 241–203

# BOOK NOTICES

**McKenny, Margaret.** 1939. Birds in the garden: How to attract them. xviii + 349 pp. 16 figs. in full color; 32 half-tones. *Reynal and Hitchcock. New York.* The book deals with the common birds of the garden and field, and of "the native plants which will attract them." Poisonous plants, such as poison ivy and sumac, are omitted. The eighteen chapters treat of the esthetic and economic value of birds, planting of the garden to attract birds, food and feeding devices, protection, bird homes, water in the garden, bird songs, care of stray birds, migration and banding, value of birds in orchard and grain fields, birds in the balance of nature, birds in city parks with list of birds observed in the parks and gardens of New York City, hunting with the camera, and bird sanctuaries. Chapter eighteen consists of lists of plants to attract birds "by sections of the country," and lists of birds attracted by these plants. These lists are based on the work of Mr. W. L. McAtee, of the U. S. Bureau of Biological Survey. The color plates are reproduced from *Bird portraits in color,* by Thomas S. Roberts, published by the University of Minnesota Press. There is a bibliography of more than three pages. The book will serve as interesting reading, as well as for reference, and appears to be unique in the field it covers. It will be of equal interest to bird lovers and to gardeners, both professional and amateur.

**Kuhnholtz-Lordat, G.** 1938. La Terre Incendiée. *Editions de la Maison Carrée, Ateliers Bruguier. Nimes.* This book is an essay on agronomy and forestry. Special emphasis is placed on the various effects and roles of fire both before clearing for agriculture and after. Several types of succession are discussed and various modifications of the natural scheme suggested for rotational practices in agriculture. The extensive bibliography should be of value to anyone interested in French literature on forestry, grasslands, and agronomy.

## A Micro-climate Recorder

The immediate problem for which the recorder here described was constructed is the study of the temperature and humidity relations inside the clothes of man, but it is felt that it may have a wider range of usefulness and this is the reason why it is published before anything definite has been achieved by means of it.

Very light recorders of temperature and other data have been utilized in meteorology. They were sent up by pilot balloons and the records were made on strips of smoked glass moved by a device reacting to the decreasing pressure, and they were to be read under the microscope.

In 1938 Weickmann described a recorder called a "Taschenthermohygrograph" built from a watch in which a chart was placed on the axle normally carrying the hour hand, and records were made on this by a bimetallic thermometer and a hair hygrometer. This instrument was too large and clumsy for our purposes.

Combining the principle of Weickmann's instrument with the micro-recording of the meteorological devices I arrived at the solution here described and figured.

The motor is the clockwork of a fairly good wrist watch 23 mm. in diameter and 5 mm. thick. It is mounted in a special box (1, Fig. 1) and arranged for winding with a key instead of the usual knob. The hole (2) for inserting the key is kept shut so as to protect the clockwork against moisture. The hour-hand axle projects into a separate compartment (3) of the box where it carries the disc (4) on which the recording instruments are mounted. This disc is shown from above in figure 2. The temperature recorder is a bimetallic spiral (5, Fig. 2), unwinding slightly by increasing temperature, connected by a fine silver wire (6) to a recording lever (7) amplifying the movement of the spiral about 3 times. The moisture recorder is a single human hair 20 mm. long (8) actuating a second lever (9). The levers are provided with very fine vertical writing points tracing lines in the smoke on the glassplate (10, Fig. 1) which closes the top of the instrument. A third writing point (11), intermediate between the two, traces a base line for reference. The box is surrounded by a rim (12) with oblong holes (13) for the elastic straps used to fasten the instrument on the body. The environmental air has access to the compartment (3) containing the recording instruments through several narrow, vertical slots cut in the circular side wall and not illustrated in the figures. These slots serve also to provide needed flexibility so that the smoked glass discs can be readily inserted and removed.
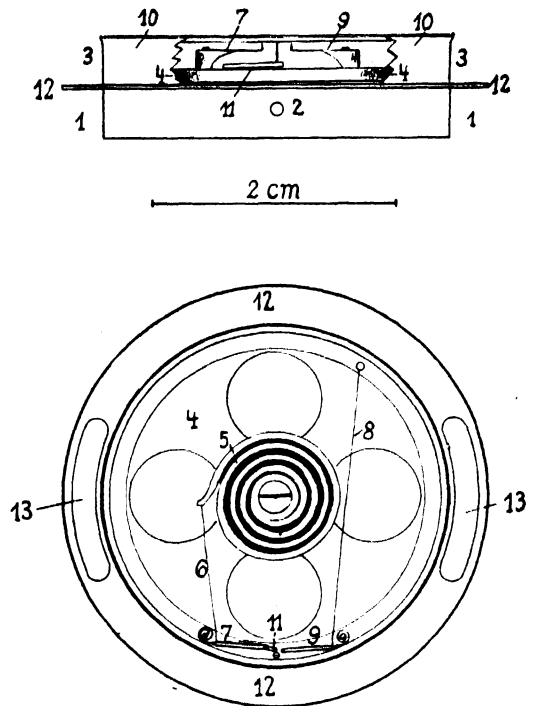


Figs. 1 (above)–2.

For each recorder 5 circular glass discs, fitting into the top of the recording compartment are provided. Each has on the upper surface an etched circle (6, Fig. 4) on which notes can be made in pencil. The lower surface of each disc is smoked *lightly* over the gas flame from a Bunsen burner with the air supply cut off completely. Smoking can also be performed over kerosene or other suitable lamps. The essential point is that the smoke coating must be uniform and only just visible. The lines traced by the writing points should be fine enough to be practically invisible to the naked eye. The smoked discs are kept in a small cardboard box separated by wire rings.

When a record is to be taken the clockwork is wound, the uppermost smoked disc is lifted out of the box by means of the sucker, presently to be described, and placed on the recorder. A pencil line is drawn from the center of the disc towards the position of the three recording points, and the date, hour and minute of beginning the record is noted on the etched area together with the number of the recorder (6, Fig. 4).

After the taking of the record, which must not of course exceed 12 hours, the glass-disc is again lifted off by means of a sucker and
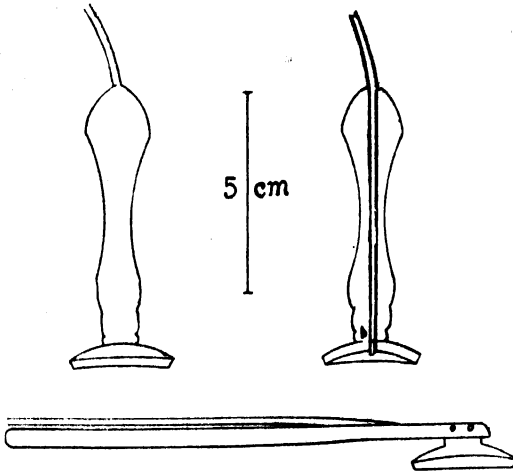
FIG. 3.

can now either be placed directly under the microscope for reading or put in a cardboard box. The clockwork should be wound before each 12 hour period.

Two separate suckers are provided (Fig. 3) each with a rubber tube passing through the handle. When this tube is closed by a finger or by a clip the sucker can hold the glass-disc which will be immediately released on opening the tube. The sucker with the flat handle parallel to the glass-plate is used for lifting the glass-discs from the microscope table.

Records are read under a microscope on a micrometer scale in the eyepiece. We have used a 1 inch objective and found a magnification by which 40 divisions on the scale correspond to about 1 mm. to be suitable. The special reading table shown in detail in figure 4 is fitted on top of the ordinary square microscope table so as to slide between 3 screw clips (1). In
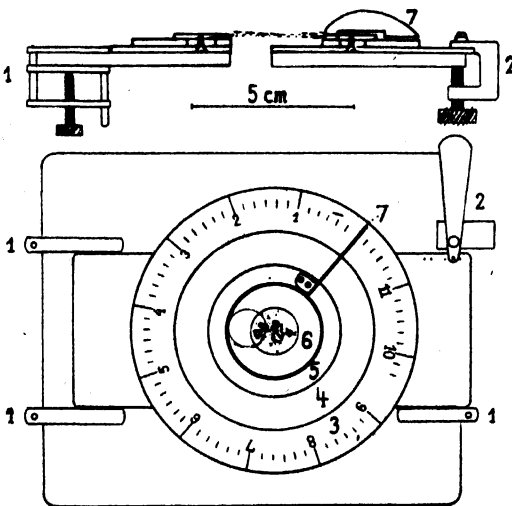


FIG. 4.

the upper right hand corner is a special clip (2) with a handle allowing the table to be moved slightly from side to side. The reading table carries two movable (3, 5) and one fixed ring (4), mounted on a rectangular brass plate with a hole which is approximately centered under the microscope objective. A disc (6) carrying a record is placed in the inner ring with the smoked surface down, and the pencil line indicating the beginning of the record pointing as nearly as possible towards the centre of the field of vision.

Looking through the microscope the beginning of the record, say of temperature (1, Fig. 5),
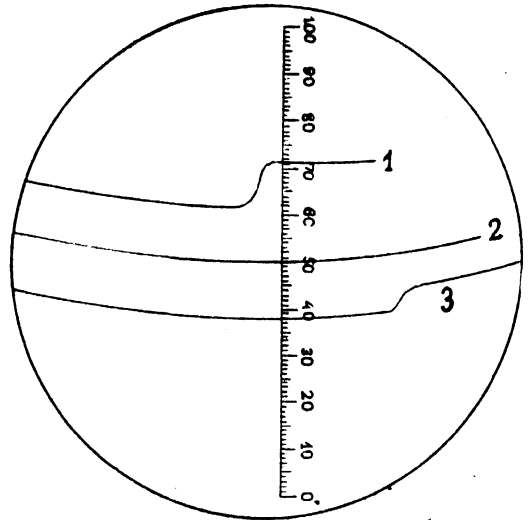


FIG. 5.

is placed on the micrometer scale by turning the inner ring by means of the pointing handle (7, Fig. 4), and then the outer ring carrying divisions in hours and minutes is turned so that the position of the pointer corresponds to the time noted on the disc (Fig. 4).

To obtain the temperature for any particular hour and minute the handle of the inner ring is now turned to the corresponding division, the table is moved so as to make the base line (2, Fig. 5) coincide with a selected division on the scale (50) and the position of the temperature line (1) read off. In figure 5 the temperature reading is 71.3. We have found it most convenient to make all temperature readings in one series and then reset the table so as to make the beginning of the moisture record coincide with the starting time noted.

Records can be measured without fixing. If it is desired to make them more permanent they are held in the sucker and the lower surface dipped for a moment in a fixing solution. We have found a 1 to 25 solution of cellulose lacquer in acetone very suitable.

From the fixed records contact prints can be made on photographic cardboard. When a series of discs is printed simultaneously, their smoke layers must be of approximately the same density.

The prints must be carefully cut out to fit into the ring of the reading table and the reading requires a fairly strong light from above.

The glass-discs can be cleaned with soap and water.

*The Calibration of the Micro-climate Recorder.*—The readings as made are in arbitrary units and valid only for that particular microscope magnification and eye-piece scale.

The readings are converted into actual temperatures and moistures by reference to calibration curves. The temperature curves for these instruments are straight lines, but separate curves must be made out for each instrument (and microscope combination). For calibration the recorder is enclosed in a small perfectly watertight metal box, and this is put alternately at two well defined temperatures maintained in Dewar vessels for periods of not less than ½ hour. As suitable temperatures 0° C. maintained by crushed ice and a temperature 1–2° C. below that of the room are recommended, but a calibration which insures at the same time that the curve is straight can be obtained by putting the recorder at, say, 35° C., letting the water cool slowly by keeping it mixed by an air current and making readings at carefully noted intervals of time.

An accuracy of ± 0.2° C. is obtained when the readings are carefully made. Most of the errors can be kept within ± 0.1° C. and the accuracy will be ample for almost all purposes. The time lag of the thermometer appears to be of the order of 1–2 minutes, but cannot of course be quite constant.

Hair hygrometers are not generally considered as instruments of precision, but a great deal can be accomplished when they are treated in the right way as described more than a century ago by Gay-Lussac. I have to admit that I have not succeeded in finding Gay-Lussac's original paper and quote only second-hand from various sources.

The increase in length of a hair with increasing moisture is not proportional with the moisture content, but is much larger in dry air. For a hair hygrometer showing 0 in absolutely dry air and 100 in saturated air Gay-Lussac has given the following values in per cent saturation corresponding to the divisions from 0–100.

Hairs should not be exposed to degrees of moisture below 20 per cent where the reaction is quite slow and the hair may become permanently altered, and Gay-Lussac prescribes further that in order to give correct results the hairs must at certain intervals be exposed to

TABLE I

| Divisions | Per cent moisture |
|---|---|
| 10 | 4.6 |
| 20 | 9.5 |
| 30 | 14.8 |
| 40 | 20.8 |
| 50 | 27.8 |
| 60 | 36.3 |
| 70 | 47.2 |
| 80 | 61.2 |
| 90 | 79.1 |
| 100 | 100.0 |

at least 95 per cent moisture. I have found these intervals to be about 3 days. When these conditions are observed hygrometers are, according to Gay-Lussac, independent of temperature and pressure and different hairs will give the same readings. The time required for a hair to attain the length corresponding to the degree of moisture is stated to be 10 minutes or less.

It is generally assumed that Gay-Lussac's figures represent averages only and that individual hairs react differently. I have thought so myself and I am not prepared to deny the statement, but the more closely I have adhered to the conditions laid down the better has been the agreement with Gay-Lussac's table for the small number of hairs (4) which I have studied closely.

I believe therefore that a safe calibration can be based upon Gay-Lussac's figures. To do this two points on the calibration curve have to be determined by experiment, while control values can be obtained by determining more points in between.

Well defined moisture percentages are established over saturated solutions of certain water absorbing salts, and from the International Critical Tables I have selected the following as suitable. $MgCl_2$ gives at 20° C., 33 per cent and at 40° C., 35 per cent moisture, $K_2CO_3$ at 18.5°, 44 per cent and at 24.5°, 43 per cent, NaCl at 20°, 76 per cent, almost independent of the temperature. When experiments are made at 22–25° the corresponding moisture percentages can be taken as 33 per cent for $MgCl_2$, 43 per cent for $K_2CO_3$, and 76 per cent for NaCl.

The pure salts are put into a suitable container (desiccators) and moistened just so much that the mass can be moulded with a spatula into giving a large irregular surface. A fluid surface makes the attainment of equilibrium too slow and must not be formed. Even when these directions are followed it takes a couple of hours to reach complete moisture equilibrium within the container.

For the determination of the two points necessary for a calibration the recorder is first

wrapped in moist filter paper in a moist chamber and after two hours wiped dry and transferred to the desiccator containing $MgCl_2$. It is advisable to take it back and forth at least twice, leaving it not less than two hours in each container. The readings obtained in a particular case (No. 5) were (at 100 per cent) 27.0, 28.0, 27.3, average 27.7, and (at 33 per cent) 47.3, 46.7, average 47.0.

The difference 19.3 is used as follows:

From Gay-Lussac's table given above a curve has been constructed from which the relative lengths corresponding to known degrees of moisture can be read off.

Column 2 in table II gives these figures for intervals of 10 per cent and also for the moistures corresponding to saturated NaCl (76 per cent), $K_2CO_3$ (43 per cent) and $MgCl_2$ (33 per cent).

TABLE II

| 1 Moisture % | 2 G.L. figures | 3 Diff. | 4 No. 5 Reading |
|---|---|---|---|
| 100 | 0 | 0 | 27.7 |
| 90 | 4.6 | 2.0 | 29.7 |
| 80 | 9.4 | 4.1 | 31.8 |
| 76 | 11.5 | 5.1 | 32.8 |
| 70 | 14.8 | 6.6 | 34.3 |
| 60 | 20.8 | 9.2 | 36.9 |
| 50 | 27.8 | 12.2 | 39.9 |
| 43 | 33.6 | 14.8 | 42.5 |
| 40 | 36.3 | 16.0 | 43.7 |
| 33 | 43.7 | 19.3 | 47.0 |
| 30 | 47.0 | 20.8 | 48.5 |
| 20 | 61.2 | 27.1 | 54.8 |

From column 2 the figures corresponding to the observed difference between 100 per cent and 33 per cent saturation can easily be calculated (multiplying by the observed differences between the readings for 100 per cent and for 33 per cent moisture and dividing by 43.7, the figure in column 2) or read off on a slide rule. The figures for the difference 19.3 of the example are given in column 3, and in column 4 the readings obtained by addition of the reading for 100 per cent moisture 27.7. Interpolations can be made by means of the table or graphically when the corresponding curve is constructed. The accuracy to be obtained varies from about 2 per cent in the lower range to about 5 per cent near the saturation point.

We have preferred graphical interpolation both for temperature and moisture and construct on millimeter paper a chart for each instrument with the readings as ordinates (each scale division = 2 mm.). For the temperature divisions on the abscissa we take 5 mm. per 1° C. from — 10° to + 40° and for the moisture

scale 20 mm. per 10 per cent moisture from 0 per cent to 100 per cent.

For many purposes recorders working over periods of 3 to 7 days would be much more useful. I have made one such which will record over a period of 7.5 days (180 hours). The length of the record is rather more convenient than the 12 hour record which appears under the microscope as too long drawn out, but the instrument has become too bulky, being 60 mm. in diameter and 50 mm. high. I have no doubt that small instruments of this type can be constructed.

Owing to present difficulties the Laboratory of Zoophysiology cannot undertake the manufacture of these recorders beyond the number which we require for our own purposes. It is fortunate therefore that Dr. Walter R. Miles of the School of Medicine, Yale University, New Haven, Conn., who wants to use them is willing to take over the manufacture.

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Bongards: *Feuchtigkeitsmessung.* München. 1926.

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ADDENDUM

The original contribution of Gay-Lussac has been found by my friend Dr. Tetens-Nielsen published in Biot: Traité de Physique Tome II, Paris 1816 as a "Supplément a l'hygrométric" occupying pages 199–208. The tables based upon the observations are to be found in tome I, p. 532–533.

The observations were made apparently on a single hair-hygrometer which was suspended in a glass container over various solutions of NaCl, $CaCl_2$ and $H_2SO_4$, the densities and vapor pressures of which were carefully determined. All the observations were made at 10° C., and Biot as well as Gay-Lussac himself apparently assume that the relation between the length of hairs and the relative degree of moisture will vary somewhat with temperature. This contention has not been confirmed by later observers, but should perhaps be investigated again.

Biot finds that the actual measurements made can be expressed very closely by a rectangular hyperbola and the tables are calculated on this basis.

## SUCCESSION ON THE NEW ENGLAND SALT MARSHES

The plant succession on one or two New England salt marshes has been noted by various investigators but so far no attempt has been made to draw up a scheme which would represent the lines of succession on the coast as a whole. These salt marshes, which may be regarded as extending from Maine to New Jersey, form a distinct group as compared with those in the Bay of Fundy or those on the coastal plain of the Southern States. A proper comparison of these three types of salt marsh cannot adequately be made unless a general scheme for each group has been prepared. This necessity has been made abundantly clear by a study of the British salt marshes which showed that they could be divided into four groups all differing from each other in edaphic characters, vegetation, and the nature of the succession. A broad survey of this nature may not advance our knowledge much farther than it is at present, but it undoubtedly serves to emphasize the major points of difference, and at the same time indicates the lines along which future research will be most profitable. It is in this spirit, therefore, that the survey of succession on these marshes has been made and in the hope that other investigators will perform a similar service for the Bay of Fundy and Coastal Plain marshes.

As a group the New England marshes are characterised by being built up of a firm marine peat in which some mud is admixed, whilst the vegetation is primarily dominated by *Spartina patens* and *Distichlis spicata*. The general succession along the coast can be outlined as:

Zosteretum
↓
Bare mud
↓
Spartinetum alterniflorae
↓
Spartineto-Distichlidetum
↓
Juncetum gerardii
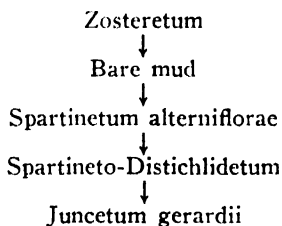
Various lines of development may occur after the *Juncus* phase, probably dependent upon local conditions. It may progress into a Spartinetum pectinatae, or a Scirpetum, or a community of *Iva frutescens* var. *oraria*, or a Typhetum latifoliae, or a Phragmitetum.

Good examples of a Phragmitetum, for example, can be seen on Cape Cod (Brewster and Barnstable marshes) and on Stratford marsh near Bridgeport, Connecticut.

In addition to the primary succession there is a secondary one to be observed in the process of pan colonisation. Steiner ('34, '35) [1] appears to

be the only previous author to have paid any detailed attention to this feature. He notes that pans may be colonised by either *Spartina alterniflora* var. *pilosa* or else by *Salicornia mucronata*, and in either case he suggests that they are followed by *Distichlis spicata* and ultimately by *Spartina patens* var. *juncea*. My observations indicate that *Suaeda maritima* may also take some part in pan colonisation.

Apart from the pans there are the secondary bare areas which have been produced by the deposit of trash or through periodic burning. These are colonised either by *Suaeda maritima* together with *Puccinellia maritima* or else by *Salicornia herbacea* (*europaea*). Throughout the whole of New England and Nova Scotia *Salicornia herbacea* appears to be primarily a secondary colonist, only occupying bare areas that have previously borne vegetation.

There are also the edges of creeks where undermining has gone on to such an extent that a definite zone of ground has sunk to a lower level than that of the main marsh. In such places there is a retrogressive succession. It is probable, too, that before the drainage ditches were dug retrogressive successions occurred in low-lying areas where water accumulated, because in such places rotting of the peat sets in and gradually it degenerates until a salt pan is formed.

For the purpose of preparing a general scheme for the New England marshes observations were made along the coast wherever possible, and they have been considered in relation to the records of earlier authors.

The above scheme is a representation of the successions to be seen on Romney marsh near Boston, Massachusetts (fig. 1). If it were not for the drainage ditches the succession from Pan type B would probably have to be regarded as reversible. It is unfortunate that the presence of the ditches has rendered a study of the retrogressive phases in the formation of these degenerate pans impossible. The principal succession on the Weymouth and Cohasset marshes is:

Spartinetum alterniflorae
↓
Spartinetum patentis
↓
Spartineto-Distichlidetum
↓
Juncetum gerardii
↓
Spartinetum pectinatae
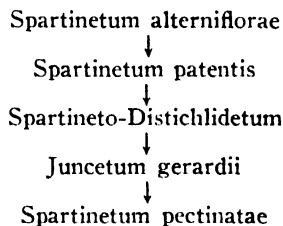
On the recolonising Scituate marshes the first

[1] Steiner, M. 1934. Zur Oekologie der Salzmarschen der nordoestlichen Vereinigten Staaten von Nordamerika. *Jahr. Wiss. Bot.* **81**: 94–202.

———. 1935. Die Pflanzengesellschaften der Salzmarschen in den nordoestlichen Vereinigten Staaten von Nordamerika. *Ber. Frei. Verein. Pflanzengeog. und Syst. Bot.* **81**.

BARE AREAS       PRISERE       PAN A       PAN B

A       B

Salicornietum herbaceae    Suaedeto-Puccinellietum    Zosteretum    Salicornietum mucronatae    Salterniflorae var. pilosae & Suaeda maritima

Bare mud

Spartinetum alterniflorae

Spartinetum patentis

Plantagineto-Limonietum

Spartineto-Distichlidetum

Spartinetum pectinatae

Juncetum Gerardii

Suaedetum maritimae

(on shrub)

Scirpetum

Panicetum dichotomoflori

FIG. 1. The successions on Romney marsh, Massachusetts.

BREWSTER MARSH

PRISERE

DEPRESSIONS

Spartinetum alterniflorae

Spartinetum cynosuroidis

Spartinetum alterniflorae var. pilosae

Plantagineto-Limonietum (+Gerardia maritima, Triglochin maritimum)

Distichlidetum spicatae

Spartinetum patentis

Juncetum Gerardii

Typhetum latifoliae      Phragmitetum

HARWICHPORT MARSH

Spartinetum alterniflorae    S. alterniflorae var. pilosae +Suaeda maritima

Spartinetum patentis

Distichlidetum spicatae (+Salicornia ambigua)

Juncetum Gerardii (+Limonium trichogonum)

Spartinetum pectinatae.

BARNSTABLE MARSH

Spartinetum alterniflorae    S. alterniflorae var. pilosae

Spartinetum patentis

Spartineto-Distichlidetum

Asteretum subulati

Spartinetum pectinatae    Spartinetum patentis

Juncetum Gerardii

FIG. 2. The Cape Cod marshes.

COLD SPRING HARBOR, L. I. (Conard, 1934)

Zosteretum marinae

Ruppietum maritimae

Spartinetum alterniflorae ———— Plantaginetum

Distichlidetum          Salicornietum

Spartinetum patentis          Suaedetum maritimae

Scirpetum

Ammophiletum
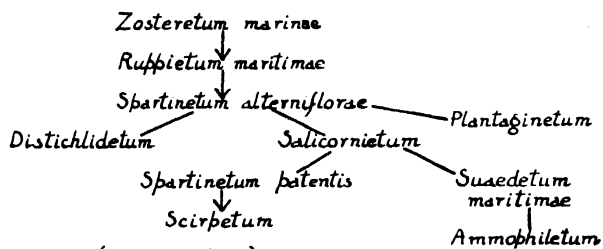
NEWHAVEN, CONN. (Steiner, 1934)

PAN A          Spartinetum alterniflorae   PAN B          PAN C

Spartineto-Distichlidetum          Spartinetum alterniflorae   Salicornietum mucronatae

Distichlidetum          Distichlidetum

Spartinetum patentis

Distichlidetum

Juncetum Gerardii

Ivetum orariae

Panicetum virgati
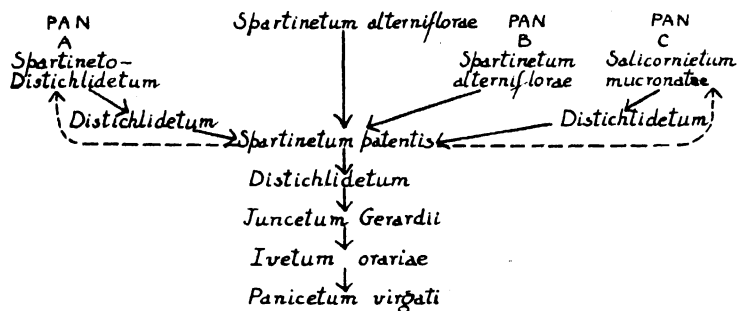
CONNECTICUT MARSHES (Nichols, 1920)

Zosteretum marinae

Spartinetum alterniflorae

Spartinetum patentis          Distichlidetum spicatae

Juncetum Gerardii
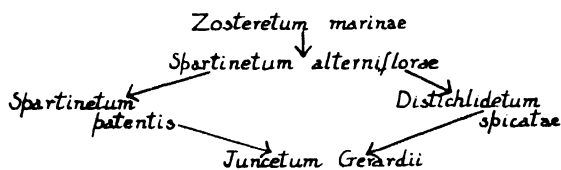
FIG. 3. Some of the New York and Connecticut marshes.

SUBSERES          PRISERE          PANS

A          B          A          B

Salicornietum herbaceae          Suaedeto-Puccinellietum          Zosteretum          Salicornietum mucronatae          S. alterniflorae var. pilosae & Suaeda maritima

Ruppietum

(before drainage?)

Bare mud

Spartinetum patentis          Spartinetum alterniflorae          Distichlidetum spicatae          (on sand and shingle)

Plantagineto-Limonietum          Salicornietum mucronatae

Spartineto-Distichlidetum          (in depressed areas)          Suaedetum maritimae

Distichlideto-Salicornietum ambiguae          Spartinetum patentis          Asteretum subulati          Ammophiletum breviligulifoliae

(on shingle)          Juncetum Gerardii          Ivetum orariae

Suaedetum maritimae          Spartinetum pectinatae

Scirpetum

Panicetum dichotomoflori          Phragmitetum          Typhetum latifoliae          Panicetum virgati

FIG. 4. The New England salt marsh successions.

three phases can be seen whilst around the edge *Juncus gerardii* persists from a previous era.

A number of marshes were visited on Cape Cod and the following successions recognised. The presence of the Spartinetum cynosuroidis at Brewster is a feature that demands further investigation (fig. 2).

Interesting features here are the greater importance of *Salicornia ambigua* and the presence of *Limonium trichogonum* in considerable quantity in the Juncetum. *Salicornia ambigua* is a very prominent feature of the southern Virginian marshes and also of the Californian marshes and it may be that the spread northwards of this species is inhibited by the winter temperatures. The occurrence of *Limonium* in the Juncetum is also a feature that one associates more with the southern Virginian marshes.

The following schemes have also been put forward by Conard,[2] by Steiner ('34) and by Nichols [3] as illustrating the succession on certain marsh areas (fig. 3).

The scheme set out below, which incorporates the information obtained from the individual marshes, is proposed as a picture of the successions that are to be found on the New England marshes. All these will not, of course, be observed on any one marsh, the presence of the different lines of development being determined by the local conditions (fig. 4).

This scheme may appear somewhat bewildering as it is very complex, but the present author has been forced to the conclusion that salt marsh succession is by no means the simple phenomenon seen by earlier authors, and that it can only be represented schematically by a complex diagram.

I would like to take this opportunity of thanking Professor Redfield and the other members of the Biological Faculty at Harvard for facilitating this work.

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# Ecologic Notes

## on the

## Violets of Alachua County, Florida

The author first studied violets in Virginia, where there were many species and numerous individuals. In comparison, the violets of northern Florida seem few and easy to distinguish.

### List of Alachua County Species

*Viola floridana* Brainerd. Florida Violet. Abundant.

*V. lanceolata* L. Lance-leaved Violet. Frequent.

*V. primulaefolia* L. Primrose-leaved Violet. Rather Common.

*V. septemloba* LeConte. Pineland Violet. Common.

*V. sororia* Willd. Large Hairy Violet. Rare.

*V. triloba* Schw. Three-lobed Violet. Common.

*V. vittata* Greene. Long-leaved Violet. Rare.

*V. walteri* House. Walter's Violet. Abundant.

*V. villosa* Walt. Recently found in the county, —a violet-flowered species of dry oak woods.

### Key to Alachua County Species

Flowers violet
  Leaves not lobed
    Leaves small and mottled..*V. walteri*
    Leaves not mottled
      Young leaves glabrous..*V. floridana*
      Young leaves hairy.....*V. sororia*
  Leaves lobed
    Found in pinelands; cleistogamous peduncles erect.*V. septemloba*
    Found in high hammocks; cleistogamous peduncles prostrate...........*V. triloba*
Flowers white
  Leaves elliptic or ovate......*V. primulaefolia*
  Leaves long and narrow
    Leaves lanceolate, 3–6 inches long; petals rounded at the tip......*V. lanceolata*
    Leaves narrower, 4–12 inches long; petals often acute at the tip .....*V. vittata*

### Ecologic Notes

The violets of Alachua County, although not so diversified as in many northern regions, nevertheless offer a very inviting field for ecologic study, especially if one could devote a period of years to it. It is not uncommon to see great colonies of these plants that have

[2] Conard, H. S. 1935. The plant associations of central Long Island. *Amer. Midl. Nat.* 16: 433–514.

[3] Nichols, G. E. 1920. The vegetation of Connecticut. The associations of depositing areas along the sea coast. *Bull. Torr. Bot. Club* 47: 511–548.

spread widely through the years in localities particularly favorable, such as the bottom of a sink or the shaded flood-plain of a river. The acaulescent species do not spread very fast by their branching rootstocks, but *V. walteri* spreads by runners almost as rapidly as a strawberry plant.

Seeds seem to be helpful in distribution chiefly where there is flooding over a low, level area or a rush of water at high levels along streams or drainage channels. The flood-plain of a river, for example, where the soil remains moist and shady, may be entirely covered for hundreds of yards by *V. floridana* in this way. I have also seen places where the soil had been removed, covered by this species so quickly that nothing but seed distribution could account for it.

The fruit is a firm capsule developed from a one-celled ovary with three parietal placentae. At maturity this capsule snaps open suddenly, its three boat-shaped valves spring back, and dozens of seeds are revealed filling the valves. There may be as many as sixty of these small, polished, obovate, pale or dark seeds, which are pinched out one or two at a time as the valves dry and fold inward on the midrib. The pinching process, operating on a smooth, sloping surface, sends the seeds several feet from the parent plant, as melon seeds are shot by pressing them between the thumb and finger. As they are light and float easily on water, they may be carried for miles during heavy rains.

Seed production varies in different species and with different seasons. The colors and markings of mature violet seeds are rather inaccurately known. Specimens seen in the herbarium are often taken from immature capsules before the true colors have had time to develop. Another source of confusion is the manner of growth of the peduncles in their younger stages and with the approach of maturity. Naturally, the plant that lifts its fruiting capsules into the air at the time of dehiscence should have an advantage. In the case of *V. floridana* the cleistogamous flowers are borne on short prostrate peduncles, but when the fruit is ripe it is raised aloft by the great elongation and elevation of these same flower-stalks.

The scarcity of fruiting capsules from petaliferous flowers in our local blue-flowered species seems almost to eliminate variation and hybridization as a fertile field for investigation. Selfing maintains a pure colony, which enlarges through the years, the chief variation appearing in the foliage about flowering time, as seen in *V. septemloba* and *V. triloba*.

Adaptation to certain soils is conspicuous in most of our species. *V. septemloba*, for example, occurs only in pinelands; *V. floridana* only in low hammocks; and *V. triloba* only in high hammocks. Opportunities for hybridization are therefore scarce, except perhaps in the

case of two white-flowered species. *V. lanceolata* and *V. vittata* occur in marshes, where their seeds may readily be distributed by water, thus forming mixed colonies in which hybrids may occur. Possibly this accounts for the difficulty we have in telling the two species apart.

An unusually fine pure colony of *V. lanceolata* was observed on April 1, 1939, east of Gainesville where a small cypress pond in the flatwoods had been drained and the area afterwards run over by fire. Several of the cypress trees had been killed; the few specimens of *Nyssa biflora* had put out new leaves; and almost the entire circle where the pond had been was green with waving fronds of *Anchistea virginica*. Mixed with the fern were flowering plants of *Erigeron vernus, Sagittaria graminea, Pilostaxis cymosa, Scutellaria integrifolia, Fuirena scirpoidea, Carex verrucosa* and *Buchnera floridana;* while many young plants of *Centella repanda, Pluchea foetida,* and various grasses and sedges were growing rapidly with the return of warm spring weather. Near the margin were a few rosettes of *Osmunda regalis,* two close colonies of *Lorinseria areolata,* some small water oaks and wax myrtles, and then the flatwoods with slash pines and their peculiar flora. Into this drained swamp had come the violets, closing in from the sides by the hundreds, until there were thousands of plants and probably a million blooms. By creeping stolons, by seed shot from shrinking capsules, by water distribution during rains, they had quickly invaded an area well adapted to them. Capsules by the dozen were raised aloft above the vernal leaves among the small white flowers, while cleistogamous flowers and fruit were developing below to bear seed after the fruits of the petaliferous flowers were gone. Here was a plant fully armed for invasion and making use of almost every facility that nature could supply. In comparison, all the other violets in this region except *V. floridana* appeared weak and ineffectual. With all this energy, however; with every opportunity for cross-pollination; and an untold number of plants; there was not enough variation, either in form or villosity, to be noticeable.

As to their reaction to light, most of our violets occur in shaded places. *V. floridana* will grow in the open where the soil is rather wet but its usual habitat is the low hammock where there is shade as well as moisture. The same may be said of our white violets, which usually grow in very wet places. Dense shade is not so favorable as medium shade; and *V. septemloba* can stand more light than most of the others.

Three of our species must be looked for in the high hammocks. *V. walteri* is by far the most abundant of these, spreading quickly as it does by long creeping rootstocks that penetrate the leaf-mold in every direction. It will move

right down to a colony of *V. floridana* growing in moister soil but the two do not hybridize, probably because not closely related. *V. triloba* is common in small, scattered colonies throughout our high hammocks. It does not spread readily by rootstocks, and the seeds fall into the dead leaves, where they do not have the advantage of flood distribution enjoyed by such species as *V. floridana*.

Violets are rarely injured by the Florida winter, which only gives them the rest they require after the long growing season. The rootstocks of our acaulescent species afford all the protection necessary during the few frosty months, and the long runners of *V. walteri* are hidden under the leaves until spring-time comes and new rosettes appear at their tips.

Drought affects the local species more than cold, but damage is largely offset by early flowering. When the late spring days arrive, with their prolonged hours of sunshine unrelieved by clouds, the crisis in the life of the violets has been safely passed, the seeds have been dispersed, and a large rosette of protecting leaves stands ready to meet the emergency. When midsummer comes there is plenty of water; dry autumn days mature the plants; and winter puts them gently to sleep.

Insects and violets appear to have little in common in this part of the world. None of our native violets are fragrant and, although the petaliferous flowers seem constructed for cross-pollination, they open before many insects are out, and appear to have little to offer the few that are on the wing. Insect pests are few, and fungi rarely do serious damage. Cows eat off the early flowers and leaves but do not ordinarily reach the cleistogamous flowers, although the crop of fruit may be greatly diminished. Hogs may uproot individual plants but can make no permanent headway against a whole colony.

The selection of local species for cultivation about the home would depend largely upon the kind of soil and the amount of water available. *V. septemloba* is most attractive, but it requires the acid soil of pinelands. *V. floridana* thrives only in low hammocks or at least where the soil is damp. The white species demand still wetter soil, and it must also be acid. The foliage of *V. walteri* is very pretty but the flowers are rather small. Perhaps one should buy plants of *V. odorata* and be done with it—unless one wishes to experiment with *V. triloba*, whose natural habitat probably approaches nearest to the ordinary shaded yard or the north side of a house. Its foliage is variously divided, the flower-stalks are tall, and the large flowers are deeply colored and highly attractive even if not fragrant.

<div align="right">

WILLIAM A. MURRILL

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# NOTES ON HOME RANGES AND POPULATIONS OF THE SHORT-TAILED SHREW [1]

Some information about the short-tailed shrew (*Blarina brevicauda talpoides*) was obtained in the summers of 1938 and 1939 during the course of a study of the home ranges and populations of the prairie deer-mouse. All of the field work was conducted on the Edwin S. George Reserve of the University of Michigan, which is located in Livingston County, Michigan.

The field work was supported in part by a grant from the Michigan Academy of Science, Arts, and Letters. The facilities of the George Reserve were kindly made available by F. M. Gaige, Director of the Museum of Zoology. P. F. Blair, Jr., and B. J. Bujak served as part-time assistants during a part of the summer of 1938.

*Ecological Associations.*—One or more shrews were found in 4 of 6 plots that were trapped in a grassland association in the summer of 1938. The grassland areas in which the plots were placed alternated with woodlots, in which the short-tailed shrew also is known to occur.

The grassland association was characterized by a more or less dense cover of blue-grass (*Poa pratensis* and *Poa compressa*) and will be designated the blue-grass association. Two and six-tenths acres of the seven-acre plot in which the shrews were most abundant were low and relatively moist and had a heavier cover of grass and other herbaceous vegetation than the remainder of the plot (Blair, in press). Other small mammals than the short-tailed shrew recorded from the blue-grass association were the mole (*Scalopus aquaticus machrinus*), weasel (*Mustela frenata noveboracensis*), thirteen-lined spermophile (*Citellus tridecemlineatus tridecemlineatus*), prairie deer-mouse (*Peromyscus maniculatus bairdii*), wood-mouse (*Peromyscus leucopus noveboracensis*), lemming vole (*Synaptomys cooperi cooperi*), meadow vole (*Microtus pennsylvanicus pennsylvanicus*), and jumping mouse (*Zapus hudsonius hudsonius*).

The short-tailed shrew primarily is an in-

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[1] Contribution from the Laboratory of Vertebrate Genetics, University of Michigan.

habitant of forest rather than grassland associations. Therefore, it should be emphasized that the present report concerns the species only in the blue-grass association in southern Michigan. In this association it is quite probable that this shrew has different habits from those it has in forest associations.

*Methods.*—Areas of blue-grass association that were more or less surrounded by forest were selected for the deer-mouse study. The plots were covered with a pattern of regularly spaced, small, live traps. Most of the traps were made of wood, and were of the single catch type. After one animal entered a trap no other could enter until the trap had been reset. Cotton nesting material was provided in each trap. The traps were baited with a mixture of seeds, of which millet, wheat, hemp, and canary seed were the principal constituents. Many field crickets (*Gryllulus assimilis*) entered the traps to feed on the seeds, and it is possible that in some cases the shrews entered the traps to feed on these insects. Of course it is possible that the shrews entered the traps merely for exploration.

Every shrew that was not dead on the first night of capture was numbered by clipping off one toe on a front foot and one on a hind foot. Each time an animal was caught the number of the trap was recorded, as were any pertinent data on behavior or sexual condition.

*Mortality in the Traps.*—Twelve of the 40 shrews trapped in 1938, or 30 per cent, were dead in the traps on the first night that they were caught. The remaining 28 individuals were trapped a total of 116 times with the loss of only 6 more animals. Of these 6, only 4 died from apparent physiological causes, as one was caught under the trap door and the other was killed by another shrew that was caught in the same trap. It generally could be expected, therefore, that if a shrew survived the first night it would survive subsequent nights in the traps. It seems evident from this that there is considerable variation in the ability of the individual shrews to survive the conditions of confinement in the traps. Of the 12 shrews that died in the traps on the first night that they were caught 10 were males and only two were females. Of the 6 that died later, one was a male and 5 were females. Four of the 5 females had recently suckled young.

In the 1939 season, 5 of the 19 shrews recorded, or about 25 per cent of them, were dead on the first night that they were taken. The other 14 individuals were trapped a total of 34 times with the loss of only one animal. This bears out the evidence from the previous season that individual shrews vary in their ability to withstand confinement in the traps.

*Sex Ratio.*—Forty short-tailed shrews were examined during the course of the 1938 season.

In determining the sex of the live shrews it was possible to force the penis of each male into view by the proper pressure on the abdomen. Of course this was not necessary with all of the shrews, as sexually active males could be identified by their enlarged testes and sexually active females by their prominent mammae. Of the shrews examined, 19 were females, and 20 were males, and the sex of one was not determined. This gives a sex ratio, on the basis of the material examined, of about 51 per cent males to 49 per cent females. In the 1939 season 8 males and 11 females were taken. Townsend ('35, p. 70) on the basis of 438 specimens found a sex ratio of 55 per cent males to 45 per cent females. Hamilton ('29, p. 131) on the basis of 93 specimens found a sex ratio of 69 per cent males to 31 per cent females. My own data and those of Townsend seem to indicate approximately equal numbers of males and females. Likewise, Lyon ('36, p. 49) believes that in Indiana the sexes are about equally divided. Hamilton's material, on the other hand, seems to indicate a preponderance of males. In this connection it should be pointed out that sex ratios calculated from material obtained by random trapping methods may be subject to a considerable degree of error. The home ranges of male short-tailed shrews tend to be larger than those of the females. Therefore, a line of traps set at random in any given area should cross the home ranges of more males than females. The total catch of males in a line consequently should be larger than the catch of females even though the two sexes are approximately equal in abundance in the area. The animals on which my sex ratios are based, although few in number, presumably represent all or nearly all of the population of short-tailed shrews on measured plots that were trapped systematically over a period of several months.

*Breeding.*—Each female shrew was examined each time it was caught to determine from the condition of the mammae whether or not it had a suckling litter at the time. A female was recorded as non-suckling if the mammae were undeveloped. It was recorded as suckling if the condition of the mammae indicated that it had an unweaned litter. A female was recorded as recently suckling if the condition of the mammae indicated that it apparently had recently weaned a litter. Some of the females apparently were pregnant, and this condition also was recorded.

In the 1938 season, the one female taken in a 7.6 acre plot between July 11 and 17 was suckling. Two of the 5 females recorded there between July 25 and 31 were recently suckling. Two of the 7 females recorded between August 9 and 16 were recently suckling, and another was both suckling and apparently pregnant. Only one of the 6 females taken during the August 24 to 30 period was suckling. Only one of

5 females recorded from September 7 to 13 was suckling. Two of the 7 females taken during the period from September 21 to 27 were suckling, and another apparently was pregnant. Although the number of individuals examined each period is quite small, it seems evident that breeding activity was low during late August and early September.

In the 1939 season, two females taken between June 8 and 15 were suckling. These were the only breeding females recorded during the season. One female during the August 6 to 12 period, three during the August 20 to 26 period, two during the September 3 to 9 period, and 4 during the September 17 to 23 period all were recorded as non-breeding.

Hamilton ('29, p. 128) found the species breeding in New York in the spring and early autumn, but found no sexual activity during July and August. Townsend ('35, p. 69) in central New York recorded pregnant and lactating females during the months of June, July, and August. Dice and Sherman ('22, p. 25) in northern Michigan recorded one pregnant female in July from a group of 26 females taken in July, August, and September. Seton ('09, p. 1124) recorded a nursing female on July 21 and a pregnant female on September 21 in Connecticut. He also recorded a breeding male at Rat Portage, Ontario, on October 20. Merriam ('84, p. 172) found two pregnant females in April in northeastern New York. Lyon ('36, p. 49) recorded that he has "taken specimens in northern Indiana that were evidently nursing in early October." Bailey ('29, p. 155) recorded a female with 5 embryos that was collected May 22, in Minnesota. All of these records point to a peak of breeding activity in the spring and another in early autumn with a period of low activity during the hot summer months.

*Home Ranges.*—The study plots were covered with a pattern of traps set in parallel lines. The traps in the lines were 60 feet apart, and in most of the 7.6 acre plot on which the shrews were found, the lines were 45 feet apart. For the calculation of the home ranges of the shrews the plot was drawn to scale on cross-ruled paper. If a shrew was caught in only one trap it was considered that, on the average, its home range would extend one-half the distance to each adjacent trap in the same line and one-half the distance to each adjacent parallel line. Thus, with the traps 60 feet apart in the lines and the lines 45 feet apart a shrew that was caught in only one trap would have a calculated home range of 2700 square feet or 0.06 acre. If a shrew was caught in two adjacent traps in the same line its home range would be twice that of the one caught in only one trap or 5400 square feet. If an animal was caught in two or more traps in the same line one unit of 2700 square feet was calculated for each of the two most dis-

tant traps and for every intervening trap regardless of whether or not the shrew was taken in it. Whenever a shrew was taken in two or more traps diagonally distant across the plot a rectangle 45 by 60 feet in dimensions (60 by 60 feet where lines were 60 feet apart) was drawn around each most distant trap. Then the outer corners of the various rectangles were connected by diagonal lines (see Blair, in press, fig. 1). The 15 by 15 foot squares included in the geometric figure thus obtained were counted to determine the area of the home range. Squares that extended only part way into the figure were counted as one-half.

The size of the individual home ranges has been calculated on a monthly basis. Each monthly range is based on the records from two alternating weeks of trapping during the month. Individuals that were caught only once or were caught only twice in adjacent traps in the course of a month are not included in the calculations of home range size, because it is obvious that only one or two catches usually would not adequately represent the size of the home range. Thirteen male ranges, based on 4.2 catches per individual per month, and 13 female ranges, based on 4.4 catches per individual per month are available. Five of the female ranges were less than one-fourth acre in extent; three were between one-fourth and one-half acre; 4 were between one-half and three-fourths acre; and the largest female range comprised 0.88 acre in September, 1938. Five of the male ranges were less than one-fourth acre in extent; two were between one-fourth and one-half acre; one was between one-half and one acre; two were between one and two acres; two were between two and three acres; and the largest comprised 4.43 acres in September, 1938. The male with the largest home range once was taken on three successive nights, on every one of which it was near a different apex of its roughly triangular home range. This indicated that the male covered virtually all of its home range in not more than three nights. Although the number of home ranges available is small, and the calculations of home range size possibly subject to some degree of error because of the possibility that some of the home ranges extended into contiguous woodlots, there is an indication that the males tend to range more widely than the females. The data also indicate that a female may sometimes range over as much as almost an acre in a month, and a male may sometimes range over as much as almost four and one-half acres. Few previous attempts have been made to estimate the size of the home range of the short-tailed shrew. Hamilton ('31, p. 97) estimated that "The range of any *Blarina* is probably restricted to an acre of ground," which agrees fairly well with my observations.

In no month was the entire area of the plot

covered by the home ranges of shrews. There always were some vacant spaces. Some individuals had home ranges that failed to overlap the range of any other member of the same sex. However, in most cases any given home range overlapped the range of one or more members of the same or both sexes. This leads me to believe that short-tailed shrews do not have "territories" which they defend against other individuals of the same species and sex. The home range of any one shrew tended to remain in the same general locality from month to month, but the shape and exact location of the home range indicated by the trapping records varied from month to month. One female was taken dead in June, 1939, within the limits of the home range that it occupied in September, 1938. This suggests that at least some individuals may occupy the same home range for a rather long period of time.

*Populations.*—Thirty-four short-tailed shrews were taken during the 1938 season in a plot comprising 7.6 acres of blue-grass association. Four other individuals were taken in another plot, and two were marked in another. In the latter two plots the shrews were taken only on the edges. In the other plot the shrews ranged over much of the area and were considerably more abundant. No shrews were caught in this plot during three days of trapping in March, 5 in April, 7 in May, and 6 in June. Three shrews were taken during the seven-day period from July 11 to 17, and 9 were taken in the period from July 25 to 31. Twelve shrews were caught in the period from August 9 to 16, and 8 were recorded during the period from August 24 to 30. Thirteen shrews were taken during the period from September 7 to 13, and 16 were caught in the period from September 20 to 27. The shrew population was disturbed to some extent by the death of some individuals in the traps, but it increased through the summer to a maximum in late September. In that period there were 2.2 shrews per acre in the plot.

In the 1939 season the area of the plot was slightly different from the previous season. In the low, moist west end of the plot there was a pond about 0.9 acre in extent, which was formed the previous winter by a change in the drainage facilities. However, the plot was extended eastward so that during the 1939 season it comprised about 9.0 acres. No shrews were taken during 4 days of trapping from April 23 to 26, 1939, nor during 7 days from May 23 to 29. Five shrews were taken during 11 days from June 8 to 18, and one was captured in the period from June 24 to 30. No shrews were taken in the period from July 23 to 29. Four shrews were taken in the period from August 6 to 12, and 7 were recorded during the period from August 20 to 26. Four were taken in the period from September 3 to 9, and 6 were caught in the period from

September 17 to 23. It is evident that the shrews were less abundant in 1939 than in 1938, for the 1939 maximum of 7 shrews or 0.8 individuals per acre in late August was considerably less than the 1938 maximum of 16 shrews of 2.2 individuals per acre in late September.

The concentrations of short-tailed shrews at particular places have been estimated by various authors. Shull ('07, p. 518) estimated two pairs per acre in a swamp in southern Michigan. Hamilton ('31, p. 99) estimated from his observations in New York that, "there could exist about four pairs of shrews to an acre in a choice locality." Seton ('09, p. 1122) estimated that there were 50 shrews to the acre in a woodland in Connecticut. The calculations of Townsend ('35, p. 67 and table 17) unlike those of previous workers were based on a systematic trapping method. However, his trapping quadrats were so small (17/80 acre) that inwandering of individuals from outside the limits of the quadrats undoubtedly caused his calculations of populations to far exceed the actual populations. This worker calculated populations of from 8 to 104 individuals per acre in 8 ecological associations in central New York. The quadrats employed by Williams ('36, p. 361) were even smaller and therefore more subject to error than those used by Townsend. Williams' quadrats were only 32.75 feet square, or about one-third the size of the smallest home range among my animals. Consequently, his calculations of as many as 299 shrews per acre obviously were subject to a high degree of error.

## SUMMARY

Short-tailed shrews (*Blarina brevicauda talpoides*) were trapped alive in some parts of the blue-grass association on the Edwin S. George Reserve, Livingston County, Michigan, in the summers of 1938 and 1939. A considerable number of the shrews were dead in the traps on the first night of capture, but most of those that survived the first night likewise survived subsequent nights in the traps. The sex ratio was about even. The condition of the females and the observations of other workers indicate a peak of breeding activity in the spring and in the autumn, and a period of low activity during mid-summer. The largest male home range comprised 4.43 acres, while the largest female range comprised only 0.88 acre. The home ranges of the shrews in no month covered the entire area of the plot. The home ranges of most individuals overlapped the home ranges of one or more individuals of the same or both sexes. Each home range tended to remain in the same general locality from month to month. In 1938, no shrews were captured before July, but in 1939, 4 individuals were taken in June.

In 1938, the shrews in an area of 7.6 acres of blue-grass association reached a concentration of 2.2 individuals per acre in late September. In 1939, the shrew population in an area of 9.0 acres, which was mostly coextensive with the area trapped in 1938, was consistently lower than in 1938 and reached a maximum of only 0.8 individuals per acre in late August.

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EFFECT OF FLUORINE ON HATCHING TIME AND HATCHING STAGE IN RANA PIPIENS

When a mass of frog eggs is collected in the field or obtained by induced ovulation (Rugh, '34) the appearance of the first cleavages is almost simultaneous. As development proceeds the several eggs usually exhibit considerable variation in the speed with which they reach a given embryological stage. Even when special precautions are taken to separate the eggs from one another, to control the temperature, to maintain the same volume of water for the same number of eggs, to provide equal lighting, and to assure a uniform environment for every egg, the time required to reach an early tadpole stage varies as much as 10 per cent (Pollister and Moore, '37).

Superimposed upon this variation is that of the precise stage at which hatching occurs (Mills, '39). This amounts to at least 10 per cent as related to total hours-to-hatching time.

Water from various sources is able to influence the rate of development and the stage at hatching, usually as separately variable processes. This first came to my attention when it appeared that tadpoles kept in running water in the aquarium room of the biology building at the University of Missouri hatched at a less advanced stage than commonly reported by others (Cameron, '36). A check of records and preserved specimens for the period 1931–1936 confirmed this finding. A few days later

Professor Mary J. Guthrie informed me that tadpoles kept in distilled water by one of her students were developing faster than controls in their native pond water. Several sets of experiments were carried out to compare the rates of development and stage at hatching in the different waters and at different temperatures.

Acknowledgments are due to Dr. Guthrie for the loan of certain series of preserved tadpoles, to Professor M. M. Ellis for making analyses of the waters used, to Professor W. E. Maneval for the bacteriological determinations reported, to Professor Daniel Mazia for the pH measurements, and to Dr. Katharine O. Mills for technical assistance and for retouching the photographs of plate 1.

The egg series here reported were obtained by pituitary injection. Fertilization was accomplished in pond water and all eggs remained in pond water for 3 hours. They remained within their jelly envelopes but were separated mechanically so that they formed a single layer in the fertilizing bowl. Eggs from a single female were then divided into three equal groups and in two groups the pond water was replaced by well and distilled water respectively. They were kept in finger bowls, 100 eggs to 100 cc. of water. Water was changed at 12-hour in-

TABLE I. *Analyses of waters used*

| Solute | Distilled | Pond | | Well | |
|---|---|---|---|---|---|
| | | p.p.m. | mm.l. | p.p.m. | mm.l. |
| Ca | | 0.1 | 0.0025 | 59.53 | 1.488 |
| Mg | | trace* | | 28.44 | 1.169 |
| Fe | trace* | | | 1.71 | 0.031 |
| Al | | | | 0.05 | 0.002 |
| Si | | | | 7.94 | 0.286 |
| S | | | | 24.60 | 0.098 |
| Cl | trace* | 0.01 | 0.0014 | 19.40 | 0.272 |
| F | trace* | | | 1.00 | 0.026 |
| Sn | trace* | | | | |
| Na | | 0.02 | 0.0009 | | |
| PO₄ | | 0.02 | 0.0002 | | |
| NH₃ | | 0.01 | 0.0006 | | |
| SO₄ | | 0.08 | 0.0008 | | |
| Specific Conductance at 25° C. | 11.8 mho × 10⁻⁶ | 122 mho × 10⁻⁶ | | 396 mho × 10⁻⁶ | |

* Trace: less than 0.001 p.p.m.

tervals. Temperature for any one series remained constant to within one degree C.

The three waters used in these experiments were (1) water from deep wells belonging to the University of Missouri; (2) water from Lefevre pond, a surface fed pond on the Missouri Campus; and (3) distilled water from a block-tin still. Table I gives analyses of these waters.

In nine series of several hundred eggs each, hatching took place sooner in well water than in distilled water and sooner in distilled water than in pond water. Three series were carried out simultaneously in April, three in October, and three in December. Numbers 1, 2, and 3 (April) were treated alike; but number 2 was studied in detail with preservation of sample groups of embryos at short intervals, while numbers 1 and 3 were kept as mass cultures in which the totals remained unreduced by withdrawals for preservation and without the effects of any "unconscious selection" of those preserved. Number 5 was intensively studied as representing the October group, with numbers 4 and 6 as mass controls and number 9 from the December group was supported by numbers 7 and 8. Experiment 5 (October 20, 1938; run at 22° C.) gave some hatching among well water eggs 6 hours before the first hatching in distilled or pond water. The first hatching in

distilled water was more than 6 hours earlier than the first in pond water. All the embryos of both groups were hatched within 18 hours. Experiment 9 (December 29, 1938, run at 18° C.) showed 100 per cent of the well, 50 per cent of the distilled and 21 per cent of the pond water specimens hatched at 84 hours after fertilization. Table II shows the times in hours after fertilization when half the embryos of a given group had hatched. It appears here that there is a specific acceleration of hatching in the well water over pond water amounting to about 14 per cent, and in the distilled water over pond water amounting to about 6 per cent.

The stage of development reached at a given time after fertilization varied in a different way. Distilled water specimens were most advanced, pond water next and well water least advanced when hatched. In Experiment 9 the tadpoles in distilled water had two or three gill filaments, prominent tail fins and tails more than half the body length; those in pond water no gill filaments, slight tail fins and tails half the body length; and those in well water no gill filaments, no tail fins, and tails less than one-third the body length, all at 96 hours after fertilization. Although first to hatch, the well water embryos were least developed at the time of hatching. This was especially evident in

TABLE II. *Comparison of "half-hatching" times. Time shown as hours after fertilization when 50 per cent of the embryos of a given lot had hatched*

| Experiment | T. C° | Well water | Distilled water | Pond water |
|---|---|---|---|---|
| No. 2 (April) | 22° | 66 hrs. | 73 hrs. | 79 hrs. |
| No. 5 (Oct.) | 22° | 67 hrs. | 73 hrs. | 78 hrs. |
| No. 9 (Dec.) | 18° | 78 hrs. | 84 hrs. | 88 hrs. |

PLATE I
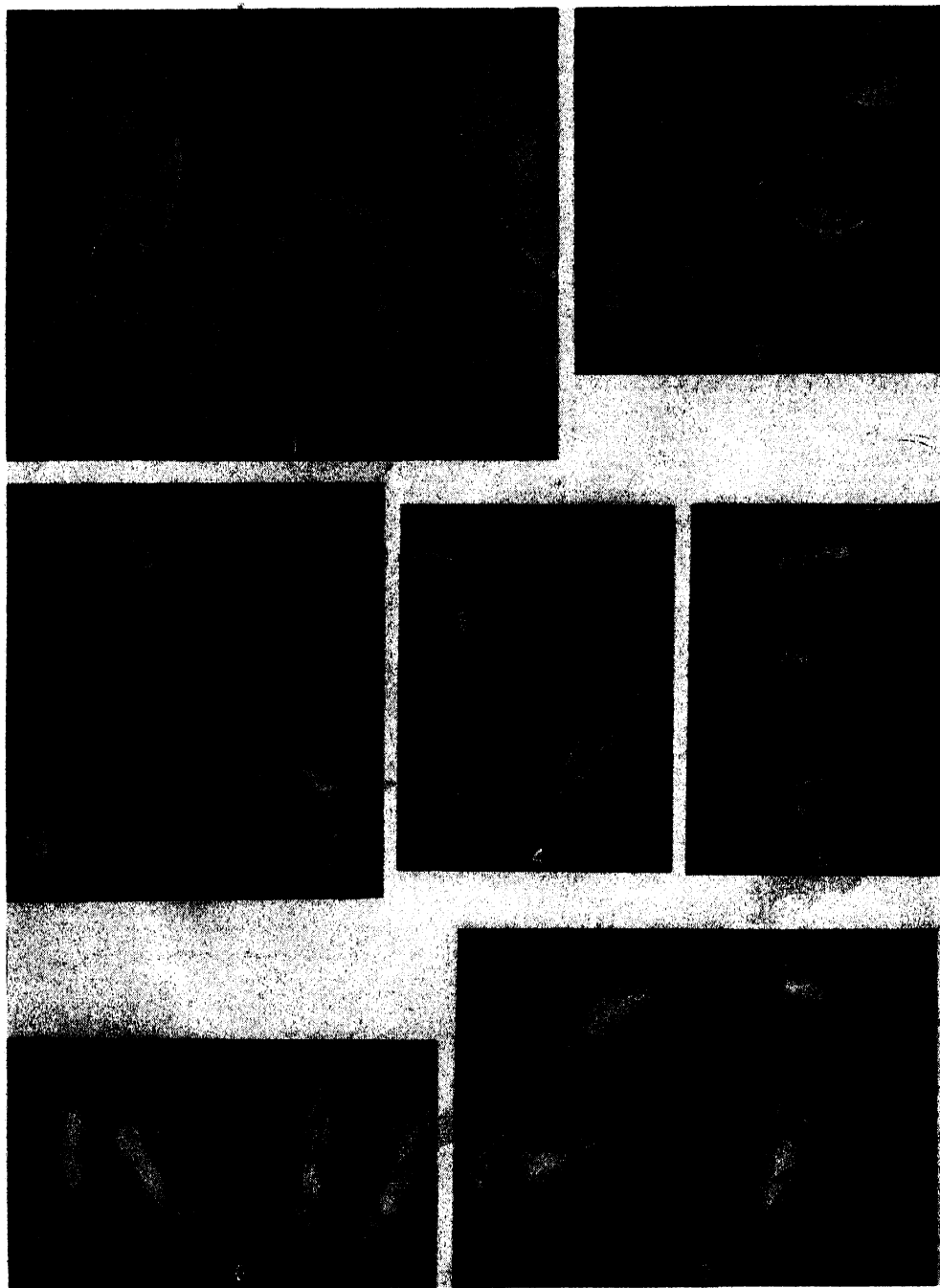


FIG. 1.  Tadpoles kept in well water containing 1 p.p.m. Fluorine.  Ca–MG present, Na–K absent.  27 hours after fertilization.

FIG. 2.  Tadpoles kept in pond water having an unbalanced Calcium–Sodium ratio. 27 hours after fertilization.

FIG. 3.  Tadpoles kept in distilled water.  27 hours after fertilization.

FIG. 4.  Same as figure 1 at 42 hours.        FIG. 6.  Same as figure 3 at 42 hours.

FIG. 5.  Same as figure 2 at 42 hours.        FIG. 7.  Same as figure 4 at 52 hours.

the comparative histology of their skin (Cameron, '36).

At 72 hours after fertilization the embryos of Experiment 5 had: distilled water—tail with fin, tail 0.3 of body length, two pairs gill filaments; pond water—no tail fin, tail 0.2 of body length, no gill filaments; well—tail bud, no gill filaments.

Figures 1, 2, and 3 are photographs of well, pond, and distilled water tadpoles of Experiment 2 (April 21, 1938, kept at 22° C.) at 27 hours after fertilization. The retardation of the embryos of figure 1 and the advanced condition of those of figure 3 can be readily noted. Figures 4, 5, and 6 represent others of the same lots of embryos at 42 hours. The differences between the pond and distilled water embryos are slight but the well water specimens are much retarded. Figure 7 shows the degree of development attained by the well water embryos of figure 4 at 52 hours. They are not as advanced as the 42-hour distilled water tadpoles of figure 6.

Muscular movement appeared in the various lots of tadpoles at about the expected stage of development and did not seem to be separately affected by the various waters.

pH (determined by quinhydrone electrode) over a range of 7.1 to 8.15 did not affect the rates of growth or times of hatching. In Experiment 9a, for example, distilled water tadpoles at 7.6 and tadpoles in distilled water made up to pH 8.15 by the addition of KOH, behaved alike and were equally advanced in comparison to well water larvae or to pond water larvae at pH 7.15.

The hatching process itself has been described for *Rana arvalis* and *Rana fusca* by Jaensch ('21). My own observations of the hatching of larvae of *Rana pipiens* agree with those of Jaensch, but have not excluded the possibility of participation by the holdfast gland in the secretion of the capsule-dissolving substance. The frontal organ, or hatching gland, a group of unicellular glands on the snout, is at its maximum development just before hatching in the larva of *Rana pipiens*. It persists for some hours after hatching (Noble, '26), but disappears after a few days (see fig. 48, p. 131,

Noble, '31). Nothing in the above indicates whether the precocious hatching of the well water larvae was due to early secretion of the "jelly dissolving enzyme" or to changes in the jelly itself. The appearance of the jelly and of the empty jelly envelope after hatching was the same in all cases. The disintegration of the empty envelopes followed the same course in each of the waters used. Needham ('31) includes a discussion of the chemistry of hatching. Sagittal sections were prepared for histological examination from a series of eggs kept half in well water and half in pond water; 6 or more embryos of each lot being fixed at 12 hour intervals from blastula to hatching-stage. These embryos were kept at 16° C. At 144 hours all the well water and none of the pond water embryos had hatched. Differentiation of the hatching glands and storage of their secretion began after the 96th hour in well water and was well established before the 108th hour. Maximum development had been attained by the 120th hour. In pond water only slight development was reached at 120 hours and at 144 hours the glands were no better developed than in the 108-hour well water embryos. Table III gives a comparison of the histological development of the glands.

Possible bacterial effects on the jelly due to greater or lesser numbers of bacteria which might have been supported by the different media were checked by the study of stained smears of the jelly from eggs of various lots. Bacteria were very numerous in all the jelly smears studied, but no difference could be established between those kept in the different waters.

Chemical analyses of the waters are shown in table I. The magnesium content of the well water is within the range of magnesium toxicity for some fresh water organisms (Ellis, '37), while the differences between rates of growth and hatching in the pond and distilled water may be due to the unbalanced ratio of Na and Ca in the pond water (Mazia, '38) or to the lower total solutes in the distilled water. The 1 p.p.m. of F in the well water was suspected of direct responsibility and sev-

TABLE III. *Comparison of histological development of hatching glands in well water and pond water embryos at 16° C.*

| Hours | Well water | | Pond water | |
| | Glands | P* + M stage | Glands | P* + M stage |
| --- | --- | --- | --- | --- |
| 96 | 0 | 16+ | 0 | 15+ |
| 108 | ++ | 17 | 0 | 16 |
| 120 | +++ | 18 | + | 16+ |
| 132 | +++ | 18+ | ++ | 17 |
| 144 | +++ | 19 | ++ | 18 |

* Stages of Pollister and Moore, '37.

eral sets of experiments were carried on to test its possible importance.

Two p.p.m. F in distilled water and 3 p.p.m. in well water produced retardation of the rates of development as compared with stock distilled water and well water. It should be noted that since the well water already contained 1 p.p.m. F the amount of F present was 4 p.p.m. This may be related to the Fluorine effect on glycolysis described by Runnström ('39).

Twenty-five p.p.m. F in pond water produced no retardation but 30 p.p.m. had an effect somewhat greater than that of 2 p.p.m. in distilled or well water. It appears then that the relatively balanced salt content or the absence of some substances in toxic amounts in the pond water allowed a F tolerance for the 'pond water that was more than ten times the tolerance in distilled or tap water.

### SUMMARY

1. The nature and amount of dissolved substances and their relative proportions exert separate and unlike influences upon the rate of development and the stage attained at hatching of normal frog embryos. Eggs kept in well water containing Fluorine hatch earlier but at a less advanced stage of development than those kept in pond or distilled water.

2. Fluorine in concentrations as low as 1 p.p.m. is able to exert a constant and measurable retardation on the rate of development and stage at hatching.

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## ANTS ON A NILE RIVER STEAMER

In a recent article (Weber, '39) records were brought together of ants found traveling or nesting on ships, mostly in the American tropics. There were nineteen species of which eight were neotropical and ten were well-known cosmopolitan ants. In July 1939, while traveling by steamer up the White Nile River and Bahr-el-Jebel in the Anglo-Egyptian Sudan for 1090 miles, several species of ants were found to be nesting on the ship.

One of these, *Euponera (Brachyponera) sennaarensis* (Mayr), of the primitive subfamily Ponerinae, is noteworthy. Arnold ('15, p. 74) states that the "economic value of this little species can hardly be overestimated, since it is exceedingly plentiful and preys unceasingly on termites. It is, however, omnivorous, since it will eagerly collect bread-crumbs, insects of all sorts, and seeds of grass." Similarly, Santschi ('35, p. 261) remarks "On ne peut donc mépriser son rôle dans l'économie agricole de l'Afrique tropicale." Throughout the Sudan from Port Sudan to the Nile and south to the Belgian Congo and Uganda borders, this ant was found to be one of the commonest insects, nesting abundantly in many areas. While not often noticed in traveling through Uganda and Kenya, where the elevations were mostly above 3000 feet, it was common at the seaport of Mombasa. Santschi has recorded it several times above 4000 feet but I failed to find it at Nairobi (5400 feet) which has almost a temperate climate. It is indeed omnivorous although insects probably constitute its chief food. A predator, the driver ant, *Dorylus (Anomma) nigricans* Ill., was observed preying upon the workers at Shambe, Bahr-el-Jebel, Sudan.

No species of ponerine ant has before been re-

corded nesting on ships. While *sennaarensis* commonly is found nesting in soil, its ubiquity about cultivations, railway stations, and other civilized places, together with the record here described, suggests that it has characteristics of a successful tropicopolitan, if not cosmopolitan, species. It may, like the South American *Iridomyrmex humilis* Mayr, be another ant observed in historic times to extend its range. Thus far it appears limited to tropical Africa and Arabia. It was common in the irrigated Arab gardens in Aden, Arabia when I visited this port August 28, 1939. Doubtless it will be found in Suez, Egypt, and could spread through the Suez Canal to Mediterranean ports. Eastward shipping might readily carry the ant to Bombay and other ports which would involve no appreciable climatic change.

On the S. S. Gedid, operating between Khartoum and Juba on the White Nile and Bahr-el-Jebel, the *sennaarensis* nested at the rear of the dining room on the upper (second) deck. Where the outside of the rear wall joined the deck, a sharp right angle was formed which evidently was seldom swept and was not seen washed down as were the side decks. The entrance to the nest was a bare hole several millimeters in diameter in the caulk between two of the deck planks close to the wall. There was no crater; an occasional sweeping or gust of wind would easily carry away the excavated material, if any. As many as fifteen workers were observed within twelve centimeters of the hole at one time. It is probable that the colony was normal in size, amounting to a few score workers. The ants carried particles of food from the dining room, gaining easy access under the screened doors, and also scavenged over much of the decks. Workers were found on the deck below, particularly on the narrow steel platform at the sides, a little above water line. Here they obtained insects and vegetal debris showered on the sides as the steamer would brush against floating islands of papyrus or the river bank itself in the sharp, narrow turns. Workers were seen on the prow at the very water line where a slight scum would occasionally gather. During the 1090 mile journey from July 1 to 14, there was every indication that the colony was securely installed and well adapted to this mode of life.

In addition to the *sennaarensis* nest there were colonies of *Monomorium pharaonis* L. and *Paratrechina longicornis* Latr. installed on the boat. The *Monomorium* workers were occasionally brought in to the table on the bread or were seen on the tablecloth and probably nested in the galley. The *Paratrechina* workers were abundant in my cabin when I came aboard in

Khartoum, scurrying in large numbers even over the berth, but their ranks were soon reduced. One of their nesting sites was in an upper corner of the wooden box around the water tank for the wash basin.

## ADDITIONAL RECORDS

An additional record of ship ants is that of *Campanotus* (*Tanaemyrmex*) *britteni* Donisthorpe ('31) from a Bibby Bros. steamer (from Indian Ocean ports) in Liverpool, England. Workers were found "in the wood casing of the refrigerator chamber, causing damage."

*Negative Records.*—By no means all ships operating in tropical waters carry ants. It appears to take some years for a ship to be seasoned enough for these insects. Search has been made unsuccessfully for ants on several ships, including the following:

M. S. Thorstrand (Norwegian), between Panama and San Francisco. A fast cargo ship commissioned only four months earlier than my passage and carrying only refrigerated fruit.

M. S. Neidenfels (German), between New York and Port Sudan, Red Sea. A fast cargo ship commissioned only four months earlier than my passage and carrying miscellaneous cargo.

M. V. Llangibby Castle (British), between Mombasa and London, August 23 to October 7, 1939. This ten year old passenger and miscellaneous cargo ship was surprisingly free of ants, in the passenger quarters at least. While waiting a week in Gibraltar for Admiralty orders, being in the first British convoy from the East in the war, fresh figs were brought from the shore in baskets which contained live worker ants of the genus *Iridomyrmex*. All seen were collected but not every ship carries a myrmecologist.

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NEAL A. WEBER

UNIVERSITY OF NORTH DAKOTA,
GRAND FORKS, NORTH DAKOTA

## MICROFILM SETS OF PERIODICALS

The Committee on Scientific Aids to Learning, President Conant of Harvard, chairman, has made a grant to cover the cost of making a microfilm master negative, on the most expensive film, of sets of volumes of scientific and learned journals.

This permits the non-profit Bibliofilm Service to supply microfilm copies at the sole positive copy cost, namely 1 cent per page for odd volumes, or a special rate of ½ cent per page for any properly copyable 10 or more consecutive volumes.

The number of pages will be estimated on request to: American Documentation Institute, care offices of Science Service, 2101 Constitution Ave., Washington, D. C.

# PROCEEDINGS

## Meeting of December 27, 1939

The Society met at Orton Hall at 8:55 A.M., President C. T. Vorhies presiding, and twenty-two members present.

The president appointed a Nominating Committee consisting of: H. C. Hanson, *Chairman;* R. E. Coker; W. S. Cooper; A. S. Pearse and Alfred Emerson; a Resolutions Committee consisting of: J. E. Weaver, C. C. Adams and J. M. Aikman. He also named H. de Forest, *Chairman* of the Western Section of the Ecological Society for 1940.

There being no further business to transact, the meeting adjourned at 9:02 A.M.

## Meeting of December 29, 1939

The Society met at Orton Hall at 3:30 P.M., President C. T. Vorhies presiding, and thirty-nine members were present. The reading of the Minutes of the last meeting was waived and reports of officers and committees were called for.

### REPORT OF THE SECRETARY

Total membership as of December 31, 1938. 731
Losses as of December 20, 1939:

Deceased ......................... 12
Cancellations ..................... 35
   Active ...................... 32
   Sustaining .................. 3

             684

Additions as of December 20, 1939:

Associate ...................... 3
Active ......................... 37
Sustaining ..................... 2
Life ........................... 1   727

Total membership as of December 20, 1939. 727

Respectfully submitted,

W. J. HAMILTON, Jr., *Secretary*

The report of the Secretary, on motion, duly seconded, was accepted.

### REPORT OF THE TREASURER

#### Ecological Society of America

*Statement of Receipts and Disbursements*

RECEIPTS

Balance, November 30, 1938 ................................................... $ 564.74
Royalty, *Naturalists' Guide* .................................... $ 64.00
Bonds ......................................................... 2.15
Dues ......................................................... 3,739.45
Miscellaneous income ....................................... .08   3,805.68

                         $4,370.42

DISBURSEMENTS

| | | |
|---|---:|---:|
| ECOLOGY | $1,911.00 | |
| ECOLOGICAL MONOGRAPHS | 599.00 | |
| BIOLOGICAL ABSTRACTS | 304.00 | |
| *Bulletin* and Secretary's office, 1938 and 1939 | 556.32 | |
| Treasurer's office | 48.65 | |
| Biologists smokers, 1938 and 1939 | 25.00 | |
| Committee, C. S. Kendeigh | 11.37 | |
| Committee, H. DeForest | 16.62 | |
| Bank charges | .65 | |
| Check lost in transit | 10.00 | 3,482.61 |

Balance, November 30, 1939 ................................................ $ 887.81

I have examined the records of Stanley A. Cain, Treasurer of the Ecological Society of America, for the year ended November 30, 1939, and certify the above statement of receipts and disbursements is in agreement with the records. The bank balance was verified with the bank. All disbursements were made by check and supported by properly approved voucher with the exception of checks to ECOLOGY and ECOLOGICAL MONOGRAPHS. One advance of $120.00 was made to the secretary on request for travel and the December Bulletin, itemization for which had not been received at the date of the audit. Receipts of dues were not traced to members accounts.

W. H. READ, *C. P. A.* (Tennessee)

January 17, 1940

Mr. Stanley A. Cain, Treasurer
The Ecological Society of America

Dean Mr. Cain:

Pursuant to your request, I have audited your records as treasurer of the Ecological Society of America for the year ended November 30, 1939, and present, herewith, the statement of receipts and disbursements.

The records were in good condition and no difficulties were encountered in the audit.

Respectfully submitted,

W. H. READ

REPORT OF THE BUSINESS MANAGER FOR THE FISCAL YEAR

DECEMBER 1, 1938–NOVEMBER 30, 1939

RECEIPTS

| | | | |
|---|---:|---:|---:|
| Cash on hand | | | $ 313.10 |
| Dr. Stanley A. Cain, Treasurer, E. S. A. | | | |
| 8 memberships 1937 at $3.00 | | $ 24.00 | |
| 50 memberships 1938 at $3.00 | | 150.00 | |
| 502 memberships 1939 at $3.00 | | 1,506.00 | |
| 48 memberships 1940 at $3.00 | | 144.00 | 1,824.00 |
| | | | |
| Subscriptions | | | |
| 1939—subscriptions | $2,326.50 | | |
| 1940—subscriptions | 590.84 | | 2,917.34 |
| | | | |
| Advertising | | | 168.00 |
| Back volumes and single numbers | | | 554.06 |

Authors payments
Cost of cuts—Frank Heyward, Jr., "April Issue" .............. $ 10.00
Excess illustrations—J. E. Weaver, "July Issue" ............... 10.00      20.00

Miscellaneous
Subsidy from Brooklyn Botanic Garden ...................... $300.00
Payment for subscription to American Journal of Botany included
in check for subscription to ECOLOGY ...................... 8.70
Reimbursement for registration fees ......................... 2.55     311.25 $6,107.75

## DISBURSEMENTS

*Printing*

Lancaster Press, Inc.

| | Issue | Reprints | |
|---|---|---|---|
| October 1938 ........................... | $ 655.37 | $ 26.62 | |
| January ................................. | 741.54 | 30.86 | |
| April .................................. | 1,251.88 | 57.56 | |
| July ................................... | 729.37 | 35.81 | |
| | $3,378.16 | $150.85 | $3,529.01 |

*Illustrating*

Ad Plate Engraving Co.

| | | |
|---|---|---|
| January ...................................... | $ 42.56 | |
| April ........................................ | 105.97 | |
| July ......................................... | 79.21 | |
| October ...................................... | 94.80 | 322.54 |

*Office expense*

| | | |
|---|---|---|
| Business—Postage ..................................... | $ 74.50 | |
| Stationery ................................... | 30.94 | |
| Wrapping paper .......................... | 7.36 | |
| Editorial—Robert E. Gregg .......................... | 41.75 | |
| Geo. D. Fuller ........................... | 28.50 | 183.05 |

*Advertising* ................................................... 54.77

*Office assistant*

| | | |
|---|---|---|
| Accounting service—December ....................... | $ 10.00 | |
| January–June .................... | 60.00 | |
| July–November .................. | 50.00 | 120.00 |

*Miscellaneous*

| | | |
|---|---|---|
| Auditing of books for the last fiscal year ...................... | $ 5.00 | |
| Payment for subscription to American Journal of Botany included in check for subscription to ECOLOGY ...................... | 8.70 | |
| Collections charges ........................................ | .88 | |
| Refund for subscriptions ................................... | 8.90 | |
| Refund on cuts—Frank Heyward, Jr. ...................... | 1.46 | |
| Expressage .............................................. | 12.43 | 37.37 |

Total disbursements ......................................... $4,246.74
Balance, November 30, 1939 .............................. 1,861.01 $6,107.75

Examined and found correct December 19, 1939.

H. P. SHOENBERNER, *Auditor*

## STATEMENT SHOWING ASSETS AND LIABILITIES

### DECEMBER 1, 1938–NOVEMBER 30, 1939

*Assets*

Cash in bank .............................................. $1,861.01

*Bills Receivable*

| | | | |
|---|---|---|---|
| Subscriptions: 1938 | ........................................ | $ 8.00 | |
| 1939 | ........................................ | 20.95 | |
| 1940 | ........................................ | 40.95 | 69.90 |

Back volumes ............................................... 7.59

Advertising ............................................ 18.00 $1,956.50

*Liabilities*

*Bills Payable*

Lancaster Press, Inc.

Printing of October issue ............................... 905.34    905.34

Balance ......................................................... $1,051.16

Circulation data as per mailing-list for the October issue:

1. Members of the Ecological Society

    *a.* U. S. A. ........................................... 497

    *b.* Foreign ........................................... 39    536

2. Paid subscribers

    *a.* U. S. A. individual subscribers ........................... 21

    *b.* U. S. A. institutional subscribers ........................... 284    305

    *c.* Foreign institutional subscribers ........................... 227

    *d.* Foreign individual subscribers ........................... 15    242

3. Advertisers ......................................... 17

4. Exchanges

    *a.* Domestic ............................................ 12

    *b.* Foreign ............................................ 112    124

5. Editorial office ........................................ 2    1226

Number of copies ordered printed per issue ..................................... 1550

C. STUART GAGER, *Business Manager*

It was moved that the report of the Business Manager of ECOLOGY be accepted. The motion was seconded and carried.

The Committee for the study of the business transactions concerned in the publication of ECOLOGY, consisting of A. H. Wright, *Chairman*, Alfred Emerson and Stanley A. Cain, then reported informally, as follows:

1. Copies of each yearly report of the secretary-treasurer on disbursements for ECOLOGY, copies of each business manager's report and copies of the reports of

all committees even remotely connected with publications were copied and scanned.

2. The following observations are made:

*a.* We have a healthy membership, desire no artificial drive but we could safely add more desirable members. Our publications, however, are our best talking point.

*b.* We could depart from our conservative advertising policy but still prefer our present course.

*c.* The format upon which Dr. Fuller

reported in December 1938 will prove very satisfactory according to both the editors and the business manager. It will save money, publish more per page and add more material to ECOLOGY with no greater cost.

3. We recommend that the present arrangements with the Brooklyn Botanical Gardens and with our Business Manager be continued as in the past. The chairman visited the business manager at Brooklyn. He saw that:

*a.* The Garden was publishing a botanical and genetical magazine for two other societies.

*b.* It has the space and good arrangements re back files.

*c.* Irrespective of considerations of ECOLOGY's predecessor PLANT WORLD, the business manager's long and satisfactory service warrants the continuation.

The report was accepted and filed and the committee discharged.

REPORT OF THE EDITORS OF ECOLOGICAL MONOGRAPHS

On behalf of Dr. R. O. Rivera, Business Manager of ECOLOGICAL MONOGRAPHS, we submit the following statement:

INCOME:

Advertising .... $ 425.00
Subscriptions .. 2,191.19 $2,616.19

EXPENSE:

Advertising .... $ 287.00
Postage ........ 10.00
Printing ....... 4,126.53 4,423.53

Excess expense over income ........ $1,807.34

*Circulation, June 30, 1939*

Paid subscriptions ..................... 221
Duke University Library exchanges ..... 30
Free exchange and complimentary ....... 26
Total ................................. 277

We also call attention to the fact that the original agreement between Duke University and the Ecological Society of America was to publish a volume of 500

pages annually. For several years we have exceeded that number by 50 to 150 pages. Dr. Shantz's Committee in 1937 recommended that we publish papers presented before Symposia of the Society. We have published them. In this connection we point out that, as space in ECOLOGICAL MONOGRAPHS is reserved for about a year and a half in advance, (1) the publication of such papers must be delayed, (2) they must be placed before papers for which space has been reserved in order of receipt, or (3) the size of the number in which symposia appear must be increased. We have adopted the last expedient, published promptly, and increased the size of volumes. An increasing number of papers is submitted for publication in the field of limnology. In order to keep the Monographs representative of various branches of ecology we have lately been obliged to refuse several good papers in that field.

A. S. PEARSE,
C. F. KORSTIAN,
*Editors*

L. R. Dice moved that the report be accepted and thanks extended to Duke University for publishing ECOLOGICAL MONOGRAPHS. The motion was seconded and carried.

J. M. Aikman moved that papers of the symposium held during the regular winter meeting be published in ECOLOGICAL MONOGRAPHS, but that this journal be kept the same size. The motion was duly seconded and carried.

REPORT OF THE EDITORS OF ECOLOGY

The 1939 volume contained 602 pages compared with 607 pages in the 1938 volume. We have sufficient manuscripts in hand for the July, 1940, issue. There are more botanical articles than zoological articles in our files at the present time.

After a careful survey and consultation with the Lancaster Press, we have adopted a new English-finish paper and a new two column format for the forthcoming vol-

ume. The savings in publication costs will be considerable and will enable the editors to publish more pages.

We recommend that a portion of these savings be used for increased editorial expenses so that the editors will not be burdened with routine work that can be handled by hired assistants. We recommend that each editor be allowed to draw up to $200.00 for the expenses of his office.

In relinquishing our editorial duties after eight years of service, we should like to thank the society and its officers for splendid cooperation in insuring adequate financial backing and help in solving the numerous problems which confront such a journal. We could not have succeeded without the splendid pioneering efforts of Barrington Moore and the constant service of C. Stuart Gager. The members of the editorial board have always given freely of their time in critically evaluating the manuscripts submitted. We have also often consulted experts in special fields and are grateful for the generous help we have always received.

We hope and expect that the new editors and the editorial board will raise the standards of excellence of the journal and give increasing publication service to the members of the society.

ALFRED E. EMERSON,
GEO. D. FULLER

The report of the Editors of ECOLOGY on motion was duly seconded, and accepted.

THIRD REPORT OF THE COMMITTEE ON A
REPOSITORY FOR THE HISTORICAL
RECORDS OF THE ECOLOGICAL
SOCIETY OF AMERICA
FOR 1939

The report of your Committee for 1937 was published in ECOLOGY (Vol. 19, pp. 328–329), and the report for 1938 (Vol. 20, p. 323). For the year 1939 the following items are worthy of record:

1. A repository for the official archives of the Society has not yet been located.

2. The cooperation of members who are interested in the preservation of these records is eagerly solicited, and they are urged to correspond with the members of the Committee.

3. Dr. John R. Dymond, Royal Ontario Museum of Zoology, Toronto, Canada, writes as follows: "I am glad to see that you have drawn attention to the desirability of preserving the historical records of the Ecological Society. I believe I have a complete file of the records of the Committee on the Preservation of Natural Conditions in Canada and Newfoundland, and also probably most of the circulars issued in connection with the Preservation of Natural Conditions in the United States."

4. Dr. George D. Fuller writes: "I have just been checking over my *Bulletin* of the Ecological Society of America and find that I have the earlier issues with the exception of Vol. 4, No. 1; Vol. 8, No. 3 and Vol. 11, No. 1. If you have these I will be glad to fill up the set and to bind the first 10 volumes (in one book) at my own expense and place it as a nucleus in a repository, when and if one is found."

5. At the Richmond, Va., meeting of the Society, Dr. Edgar T. Wherry expressed his willingness to inquire about the official correspondence of Dr. John H. Harshberger, a former Chairman of the Organizing Committee when the Ecological Society was organized. Doctor Wherry has located "four scrap books which presumably contain all significant correspondence he had while President of the Ecological Society. These are available to the Society just as soon as it is decided how and where such records are to be kept. I will be glad to send them by express whenever desired."

6. Until a repository is located, the Chairman will provide storage for signed and dated photographs of former officials of the Ecological Society.

Your Committee recommends that it be continued.

GEORGE D. FULLER
ROBERT F. GRIGGS
CHARLES C. ADAMS, *Chairman*

This report, on motion, was duly seconded and accepted.

## REPORT OF THE COMMITTEE ON SUMMER SYMPOSIA

In the absence of the chairman, Dr. Paul B. Sears, no report was given at the meeting but Dr. Sears later forwarded the following report.

This is to advise the Society that the following symposium was held at Milwaukee on Wednesday morning, June 21, 1939:

1. *The Relation of Game Management to Land Use.* Aldo Leopold, University of Wisconsin.
2. *Geography and Land Use.* K. C. McMurray, University of Michigan.
3. *The Economist's Approach to the Problem of Ecology.* George S. Wehrwein, University of Wisconsin.
4. *The Broader Social Implications of Land Use in the Cutover Region.* Raphael Zon, Lake States Experiment Station, St. Paul, Minnesota.

The papers were excellent in quality and were received with close attention by the audience which included a large number of foresters. Permission to publish the papers in the *Journal of Forestry* was requested by its editor, Dr. Henry Schmitz, and the collected papers appeared in the *Journal of Foresty* for September, 1939.

## REPORT ON SUMMER MEETINGS OF THE WESTERN SECTION E. S. A.
### 1938 AND 1939

The two summer meetings of the Western Section E. S. A., at San Diego, 1938, and Stanford University, 1939, have been reported in *Science* and in the *Bulletin* of the E. S. A. It is desired to add a few additional remarks for the business meeting at Columbus.

These last two summer meetings were, of course, considerably smaller than the national meeting of the summer of 1937

at Denver. Both the Pacific coast affairs presented, however, series of interesting and valuable scientific papers in animal and plant ecology.

The summer of 1939 was extraordinary in that, probably because of the Fair at San Francisco, a number of meetings, other than those of the Pacific Division A. A. A. S. at Stanford University, were held throughout the summer, at Stanford University, San Francisco, at the University of California at Berkeley, some even running concurrently. This made the organization of a satisfactory program for the Western Section E. S. A. at Stanford difficult; most of the foresters, for instance, preferring to reserve their papers for a later meeting at San Francisco. Especial efforts were made to have the E. S. A. adequately represented at the A. A. A. S. at Stanford, it being deemed highly desirable that ecology be furthered by all possible means in this part of the country.

The undersigned, as chairman of the Executive Committee Western Section E. S. A. for the Stanford meeting, presents the financial statement of the Western Section for the period January 1–December 18, 1939.

This amount includes cash expenditures only. The actual work includes an unknown number of hours of typing by students, for which no expenditure was made and no record of hours kept. The stationery used was mainly that of the university. Please note that the total cash expenditure is about double that for the summer meeting of the previous year at San Diego. Rather early in the organization of the E. S. A. program for the Stanford meeting it began to be realized that, if the affair were to be properly representative, a considerably higher expenditure than usual would be necessary. The chairman determined that he would go ahead and try to make the affair successful without endeavoring to obtain official sanction for a higher expense, by means of paying himself for whatever expense he incurred above the usual amount.

Therefore, for the current year, the total of $32.72 is to be divided in two, and the total expense for the E. S. .A is $16.36. There is on hand about 90 cents in stamped envelopes.

> H. de Forest, *Chairman*
> For the Committee Western Section
> E. S. A. for Stanford meeting 1939
>     C. T. Vorhies, Arizona
>     J. J. Kittredge, Jr., California

C. C. Adams moved that the report be received and filed and the treasurer authorized to pay the entire bill. The motion was seconded and unanimously passed.

## The Committee on the Preservation of Natural Conditions

### Report for 1939

No major campaign has been conducted during the year, and no claims have been submitted for payment to the Treasurer of the Society. In view of the fact that the necessity for extensive correspondence may arise at any time, however, the Chairman asks that the current appropriation of $50 in addition to the royalties accruing from the *Naturalists' Guide* be continued for the year 1940.

Some of the activities of the Committee and its chairman may be reported at this time. (1) There has been organized during the last few months the *Grassland Research Foundation,* a corporation founded for the purpose of fostering the preservation of grassland areas and the prosecution of research in connection with them. The corporation is open to all who may be interested in its objectives, and it is hoped that many of those concerned with the preservation of natural conditions may join with this organization. The chairman is temporary president and the secretary is Dr. J. M. Aikman. (2) The chairman has been in touch with various members of the Soil Conservation Service and has acted in an advisory capacity with respect to the establishment of a policy involving the preservation of typical areas of value for wildlife in connection with land utilization and other projects. He has also participated in reconnaissance surveys of such areas. (3) An investigation of the possibilities of the preservation of a unique cave at San Marcos, Texas, led to the appointment of a local Committee but no further progress can be reported at this time. The same remark applies to the Singer Wildlife Refuge in Louisiana. Attention to these areas was called by the Committee for the Study of Plant and Animal Communities. (4) There has been some correspondence with members of Congress and others in regard to the proposed John Muir National Park in California. (5) Activities in connection with last year's recommendation as to the proposed Grasslands National Monument in southwestern South Dakota and adjacent Nebraska have been continued. (6) Efforts toward the preservation of a unique nesting area of herons, anhingas, etc., in southeastern Oklahoma have failed because of the activities of "timber pirates" in the destruction of the large cypresses of the tract. (7) State and regional committees and members of the Society in general are urged to send to the chairman suggestions as to matters related to the preservation of natural conditions. It is especially desirable that projects in which the committee may assist be brought before it.

> A. O. Weese

Dr. Weese unfortunately could not attend the Columbus meetings. He asked that the Executive Committee of the Society set aside a reserve fund of $50 plus the amounts accruing from the royalties of the *Naturalists' Guide* during 1939 and 1940, to be used if and when needed by the Committee on the Preservation of Natural Conditions.

## REPORT OF THE COMMITTEE FOR THE STUDY OF PLANT AND ANIMAL COMMUNITIES

During the past year this committee has continued its interest in listing and studying areas suitable for preservation in Central America and the West Indies and in expanding the list for North America to include smaller areas. A report has been prepared by the former chairman of this committee, Dr. V. E. Shelford, and is ready for publication. It is entitled "List of reserves that may serve as nature sanctuaries of national and international importance, in Canada, the United States, and Mexico. Suggestions as to their improvement and management are included."

The committee's main efforts have been expended with the work of the special sub-committees concerned with buffering existing reservations, with the establishment of new large areas, and with the preservation of small fragments of original biotic communities. Most of these sub-committees are active and are in touch with their projects.

The question of the desirability of Admiralty Island for National Monument or Park status for the protection of the big brown bears has been studied rather intensively but in a preliminary manner and since the problem here is related to the use of Glacier Bay National Monument the chairman of this sub-committee has agreed to continue the study.

This committee has cooperated with the Committee on the Preservation of Natural Conditions in the United States and has made recommendations concerning the preservation of Ezell's Cave in Texas, the Singer Forest tract in Louisiana and the Wind River Region in Wyoming.

In order to broaden the committee's contacts and sources of information an effort has been made to interest other organizations in having representatives on the committee to act in an advisory capacity. The number of these associated organizations has been increased from four to twelve and others may be added in the near future.

A financial statement of the expenses incurred during the present fiscal year follows:

| | |
|---|---|
| Mimeographing | $ 0.96 |
| Typing | 6.00 |
| Postage | 4.41 |
| Total | $11.37 |

Respectfully submitted,
S. CHARLES KENDEIGH, *Chairman*

Dr. Kendeigh asked that $50 be set aside for his committee to meet current expenses. L. R. Dice moved that the report be accepted and that the requested amount be set aside for both committees. The motion was duly seconded and passed.

## REPORT OF THE CONSTITUTIONAL COMMITTEE

At the Richmond 1938 business meeting the president appointed a Constitutional Committee to "harmonize the present Constitution, and that the Committee be further authorized to propose any additional amendments or modifications to the Constitution which are considered necessary."

The first function has been virtually performed, namely harmonizing the original constitution with previous changes, amendments, by-laws *et cetera* and this will be presented to the Secretary for publication and circulation to the Society within the coming year.

The second function has been approached cautiously since change in the constitution requires close and extensive consideration. During the past year the following suggestions have come to my attention:

1. Change in the existing organization of the society to government by a Board of Directors so that: (*a*) there would be less break in continuity of purpose and policy, (*b*) more representation of societal

membership not at the final business meeting, (c) more representation by younger men, (d) elimination of some of the routine business ordinarily transacted at a business meeting.

2. To facilitate the society holding land for natural areas.

3. To facilitate the accumulation of endowment to (a) make grants-in-aid to ecological research of members so applying, (b) set up scholarships in ecology, (c) aid in publication of research papers.

4. To facilitate preservation of natural conditions.

5. To examine the feasibility of changing: the fiscal year of the Society, and the election of officers.

You will understand that this is a condensed summary of suggestions—some of which have been proposed by members of the Committee and some by members of the society who have been interested in the work of the Committee—and that they embrace, as a whole, many important changes.

On due consideration, and after informal conversation with many members, your Committee feels that further study is necessary before making definite suggestions to the Society. Therefore they propose:

1. That an informal conference be held on this general subject to formulate a series of suggestions.

2. That these suggestions be published in the Bulletin of the Society in the form of a questionnaire.

3. That the Society then vote on the results of the questionnaire at the 1940 meeting.

Apparently this would be the best way of obtaining the majority opinion of the membership.

4. That to perform this task the present committee be continued.

Respectfully submitted,
ORLANDO PARK, *Chairman*

It was moved and seconded that the re-

port be accepted and the committee be continued. The motion was passed.

REPORT OF THE REPRESENTATIVE OF THE
SOCIETY ON THE COUNCIL OF THE
UNION OF AMERICAN BIO-
LOGICAL SOCIETIES

The Council of the Union of American Biological Societies at 4 P.M. Thursday, December 28, 1939. The following items were reported:

1. Oscar Riddle stated that the Union's new periodical "American Biology Teacher" was subscribed for by 2200 members in Secondary Schools, in 22 states and Canada.

2. Dr. Weinich reported a $125.87 balance in the general funds of the Society and a balance of $653.43 of the Carnegie Fund.

3. John E. Flynn, Editor in Chief of BIOLOGICAL ABSTRACTS, stated that 1200 periodicals are now being regularly abstracted and that the annual indexes have been brought up to date and finally, that BIOLOGICAL ABSTRACTS is now solvent and gives every promise of remaining alive. The future, however, may be bad due to the present European situation since 40 per cent of BIOLOGICAL ABSTRACTS' income is derived from foreign sources.

4. George W. Hunter, III, called attention to the new "Thirty per cent plan" for societies—that if 30 per cent of any societies membership subscribe to a section of B. A., the section being optional for every member, the price for that subscription will be reduced by one dollar.

5. H. P. Barss proposed an amendment to the constitution of the Union whereby individual memberships could be obtained. After prolonged discussion it was suggested by President Cowdry that the proposal be further studied before action was taken.

Respectfully submitted,
ORLANDO PARK

The report was duly accepted.

REPORT ON THE NATIONAL RESEARCH
COUNCIL

Dr. R. E. Coker said that although he
was not reporting for Doctor Frison, rep-
resentative of the Society on the National
Research Council, he would mention two
activities of the Council which Doctor
Frison, were he present, would undoubt-
edly discuss as of special interest to the
Society. The Committee on Ecology of
Grasslands, of which Doctor Shelford
was so long Chairman and director, has
recently centered its efforts on two major
objectives: The establishment of a large
preserve of grasslands comparable to the
great forest preserves and some of the
National parks, and the provision of
smaller research areas convenient to the
chief universities and agricultural colleges
in which grassland research is particularly
featured. In respect to the former ob-
jective, the National Park Service has re-
cently set up a project entitled "A Grass-
lands National Monument," in the hope
that an adequate area may be acquired in
northwestern Nebraska and southeastern
South Dakota. The Department of In-
terior asked the National Research Coun-
cil for an expression of opinion and the
request was referred to Dr. Paul B.
Sears, now Chairman of the Committee
on Ecology of Grasslands, who after con-
sultation with the several members of the
Committee and a good deal of corre-
spondence prepared a report. This re-
port was approved by the Division of Bi-
ology and Agriculture and the Council
and was transmitted by the Chairman of
the Council to the Department of Interior
with one or two additional comments, in-
cluding the proposal that it might be de-
sirable at the proper time to have a con-
ference of Government officials of the
Departments of the Interior and Agricul-
ture, state officials concerned, and scien-
tific specialists to consider the many and
complex scientific problems that unavoid-
ably would be involved in the administra-
tion of such an area. Copies of this let-
ter are available to members of the So-

ciety interested in the grasslands problem
by application to the Division of Biology
and Agriculture, National Research Coun-
cil, Washington, D. C. Doctor Coker re-
marked that, although there was not
complete unanimity of opinion in the
Committee regarding every feature of the
report (size and location), the animal
ecologist and the great majority of plant
ecologists were in complete agreement. It
was thought that the report as transmitted
would be acceptable to all. The Commit-
tee will continue to work toward the sec-
ond objective—the setting up of a number
of small research areas with appropriate
location.

The other activity of the Council dis-
cussed was the work of the Committee on
Coöperation with Barro Colorado Island
Laboratory, conducted by the informally
organized Institute for Research in Tropi-
cal America. This is the only biological
laboratory for tropical research under the
American flag and it has had a remark-
ably successful career both in the service
it has rendered to individual biological in-
vestigators, including many ecologists, and
in its productiveness of publications re-
sulting wholly or in part from work done
at the station. The location of the station
on Barro Colorado Island in the Canal
Zone gives it features of uniqueness and
affords exceptionally favorable opportuni-
ties for biological research in the tropics.
The future of this station seems precari-
ous so long as it continues to have such
an informal organization. After careful
study the Committee proposed a Federal
charter for the laboratory and prepared
the draft of a bill to be presented in
Congress. The bill, it may be said, has
met the hearty approval of the National
Research Council and the National Acad-
emy of Sciences, and it has been approved
with only slight editorial revision by the
Government departments concerned: The
Department of Agriculture, the Depart-
ment of War, the Smithsonian Institu-
tion, and the Treasury Department. The
bill is expected to be introduced into
Congress by Senator Harry F. Byrd early

in January. In brief, it provides for a plan of organization something like that of the Smithsonian Institution, the governing board to consist of the Secretaries of Agriculture, War, and the Smithsonian Institution, the President of the National Academy of Sciences, and three prominent biologists to be selected by the President of the Academy of Sciences with the approval of the three secretaries. Copies of this bill may be obtained upon application to the Division of Biology and Agriculture, National Research Council, Washington, D. C.

## REPORT OF THE COMMITTEE ON THE SALE OF THE NATURALISTS' GUIDE

Dr. C. T. Vorhies spoke at some length regarding the disposition of the remaining unbound copies of the NATURALISTS' GUIDE. As there was no unanimity of opinion expression on the sale or disposition of the remaining guides, it was left to the Executive Committee to pass final judgment on the matter.

## REPORT OF THE RESOLUTIONS COMMITTEE

### I

Through press notices it has come to the attention of the Ecological Society of America that some 18,000 acres of land in the Wind River area in Wyoming are being considered for purchase under the Pittman-Robertson Act by the Wyoming Game and Fish Commission. Our investigation shows that the Owl Creek range in this area, extending eastward from the Washakie National Forest, affords the best winter range for elk on the east slope of the Rocky Mountains in Wyoming. It is well known in the West that suitable winter range is one of the important needs for elk and other big game. The Ecological Society of America therefore recommends the purchase of such lands under the Pittman-Robertson Act, and commends the Wyoming Game and Fish Commission for its wisdom and fore-

sight in considering the purchase of lands in this area as part of their game management program.

Be it resolved that copies of this resolution be sent to the Chief of the U. S. Biological Survey, and to the Wyoming Game and Fish Commission, and made a record in the minutes of the Society.

### Winter Elk Range

WHEREAS, the condition of the winter and summer range of the Yellowstone Elk Herd has long been an acute problem, and

WHEREAS, careful study of the problem shows the need of additional natural winter range that may be secured adjacent to the Washakie National Forest, Wyoming,

THEREFORE BE IT RESOLVED, that the Ecological Society of America recommends the purchase under the Pittman-Robertson Act of lands adjacent to the Washakie National Forest, thus providing additional winter range for the elk.

BE IT FURTHER RESOLVED, that copies of this resolution be sent to the United States Forest Service, the United States Biological Survey, the United States Park Service, and the Wyoming Game and Fish Commission.

### Canal Zone Biological Area and Barro Colorado Biological Station

WHEREAS, the scientific work on the tropics conducted at the Barro Colorado Biological Station has been of great value, and

WHEREAS, the station has not been conducted upon a permanent basis or foundation,

THEREFORE BE IT RESOLVED, that the Ecological Society of America heartily approves of the proposed bill, to be presented to Congress, authorizing the permanent establishment of the Canal Zone Biological Area and Station.

FURTHER BE IT RESOLVED, that a copy of this Resolution be sent to the National Academy of Sciences.

## Resolution

WHEREAS, much of the credit for the success of the 1939 meeting of the Ecological Society of America may be attributed to the favorable environment of the city of Columbus, and

WHEREAS, the excellent facilities of both the University and the city have been generously placed at our disposal,

THEREFORE BE IT RESOLVED, that the Ecological Society of America expresses to the Local Committee its appreciation of these courtesies.

> J. E. WEAVER, *Chairman*
> CHARLES C. ADAMS
> J. M. AIKMAN

### REPORT OF THE COMMITTEE ON NOMENCLATURE

In the absence of the chairman, Dr. H. Hanson, no report was given. Dr. C. F. Korstian said that this committee was active up until a few months ago and it was planned to continue through 1940.

### REPORT OF THE COMMITTEE ON NOMINATIONS

The Nominating Committee makes the following report:

Since Dr. Alfred Emerson and Dr. George Fuller are resigning as editors of ECOLOGY, it became necessary to nominate new men for these offices. The president of the Society, Dr. Charles T. Vorhies, added two members to the Nominating Committee to assist particularly in the selection of these editors. The additional members to the Nominating Committee are Dr. Alfred Emerson and Dr. A. S. Pearse.

The following nominations are recommended by the Committee to the Society:

*President:* Francis Ramaley.
*Vice-President:* Orlando Park.

*Member Executive Committee:* A. O. Weese.
*Representative Union American Biological Societies:* H. J. Oosting, C. L. Hubbs.
*Editorial Board Ecology:*
> Botany—D. B. Lawrence, H. G. Stoddart.
> Zoology—Paul Welch, R. Bennitt.
*Editorial Board Ecological Monographs:*
> Botany—J. W. Weaver, S. A. Cain.
> Zoology—Z. P. Metcalf.
*Zoological Editor of Ecology:* Thomas Park.
*Botanical Editor of Ecology:* Francis Ramaley to complete Fuller's term (one year).

> Respectfully,
> HERBERT C. HANSON, *Chairman*
> R. E. COKER
> ALFRED E. EMERSON
> A. S. PEARSE
> WM. S. COOPER

A. H. Wright moved that the nominations be closed. This motion was duly seconded and carried. The secretary was authorized to cast a unanimous ballot. The officers named in this report were declared elected.

In view of the unavoidable absence of the newly elected president, Dr. C. T. Vorhies continued in the Chair and called for new business.

Dr. L. R. Dice moved that a special committee be appointed by the outgoing president, under advisement of the Desert Laboratory at Tucson to determine what might be done. It was earnestly urged that this worthwhile project be continued. The motion was seconded and carried.

There being no further business, it was moved and duly seconded that the meeting stand adjourned. The motion was carried. Adjournment at 5:31 P.M.

W. J. HAMILTON, JR., *Secretary*

# AN EXPERIMENTAL STUDY OF CERTAIN QUANTITATIVE PLANKTON METHODS [1]

ROBERT A. LITTLEFORD, CURTIS L. NEWCOMBE, AND BOLAND B. SHEPHERD

*Chesapeake Biological Laboratory and University of Maryland, College Park*

O what an endlesse worke have I in hand,
To count the seas abundant progeny,
Whose fruitfull seede farre passeth those in land
                    Spenser's "Faerie Queene"

Ecologists in their studies of biotic communities are forever *number* conscious. Likewise, in their interpretation of biotic factors in an environment, they feel definite need for exactitude of numerical expression and for interpretations based on results that have been subjected to critical statistical treatment. This need prompted the observations and experiments herein reported.

The steps in the plankton procedure described are considered in the light of their suitability for use in shallow (to about 60 meters) waters and also in handling large numbers of samples per week for quantitative as well as qualitative analyses. The purpose of the study has been to analyze in detail the possibilities for numerical error inherent in a single, commonly employed method of plankton study rather than to provide a comparative treatment of two or more accepted procedures. It is pointed out that the purpose of a plankton study is quite as important in deciding on the acceptability of a method as the accuracy of the method itself. An attempt is not made to review the extensive literature which treats of quantitative methods for measuring the diverse types of plankton life. Obviously, many forms require special procedures depending on their distribution,

[1] Contribution number 37 of the Chesapeake Biological Laboratory.

size and abundance. Passing reference is made to the works of Apstein ('96), Brandt ('99), Allen ('19), Birge and Juday ('22), Robert ('22), Allen ('22), Kreps and Verjbinskaya ('30), Gardiner ('31), Gran ('32), Phifer ('33), Harvey ('34), Gran and Braarud ('35), Steemann Neilsen ('38), and Hentschel ('38). The successive steps taken during this study are described in an effort to contribute to the concept of quantitative accuracy as applied to plankton analyses.

The consideration given to the methods employed and tested during this study involved a critical analysis of the several current methods of collection and concentration of material. The regional conditions as well as the immediate purposes of the plankton studies at the Chesapeake Biological Laboratory have dictated the adoption of the Foerst plankton trap for the collection of material for the analysis of macrozoöplankton populations and the use of a water bottle sample—volume about 350 ml.—for the analysis of microplankton populations, rather than either the tow net or pump method of collection. The water bottle sample was centrifuged as described by Gran ('32) except that a Foerst electric centrifuge was used in place of the common clinical centrifuge. It was decided to use the Sedgewick-Rafter cell for census purposes after careful attention had been given to the pigment method of Kreps and Verjbinskaya ('30) and Harvey ('34), the settling method of Allen ('30), the drop method of Hensen ('87), the precipitation as well as the several volumetric methods.

## MATERIALS AND METHODS

Samples were collected from water at the Laboratory pier in Solomons Island, Maryland, during the months of July and August, 1937, 1938 and during April, 1939. The material from the forty-five liter contents of the Foerst plankton trap was concentrated into a sample of approximately fifty milliliters to which about two milliliters of neutralized commercial formaldehyde (pure 40 per cent formalin) were added for preservation. The concentration is effected by means of a small cone-shaped plankton net (No. 20) leading from the bottom of the trap proper to the so-called plankton bucket, cylindrical in shape, with walls consisting of plankton netting of similar mesh.

Samples for centrifuging and for chemical analysis were collected in the same Nansen-Knudsen water bottle. To each sample of approximately 350 ml., 5 ml. of neutralized formalin were added.

In order to determine the efficiency of the plankton trap, approximately one liter of water, which was strained through the trap net, was collected and treated in the same manner as the water bottle samples.

*Centrifuging.*—The water-bottle-centrifuge samples and the plankton-trap-centrifuge samples, centrifuged with a Foerst Electric Centrifuge (20,000 R.P.M.), were concentrated to about fifteen ml. The speed of the centrifuge varied somewhat with the variation of the current. The water was passed through the centrifuge at the rate of about one liter per twelve minutes. By re-centrifuging at the rate of one liter per eighteen minutes, a liter of water which had already been centrifuged at the rate of one liter per twelve minutes, it was found that about five per cent of the original amount of plankton had gone through the centrifuge. On the third centrifuging of one liter during fifty-eight minutes, about one-tenth of one per cent of the original amount of plankton was found to have gone through the centrifuge during the thirty minutes (18 + 12 min.) centrifuging.

*Counting.*—The Sedgewick-Rafter cell was used for the quantitative determination of the samples due to the fact that the investigation deals with the macrozoöplankton and microplankton, both types of which may be studied with a reasonably high power of magnification—namely, $\times$ 210 (8 mm. objective). The procedure involved the removal of 1 ml. of the concentrate to the Sedgewick-Rafter cell (capacity 1 ml.) for counting.

The two magnifications employed during different phases of the study were $10 \times 10$ and $10 \times 21$. The calibration of the eye piece micrometer is given below.

| Magnification | Area measured by micrometer |
|---|---|
| 10 × 10 | 1.00 cubic millimeter |
| 10 × 21 | 0.48 cubic millimeter |

Two formulas were used in making the calculations. The formula for calculating the number of organisms in one liter of water by the plankton trap-Rafter cell method is:

Organisms per liter of water = (Average number of organisms per area) $\times$ (number of areas in Rafter cell) $\times$ (mls. in concentrated sample representing one liter of Bay water)

Areas in Rafter cell (using 10 × 10 magnification) $= \dfrac{1000}{1} = 1000$

Areas in Rafter cell (using 10 × 21 magnification) $= \dfrac{1000}{0.48} = 2083.3$

Mls. in concentrated sample representing one liter of water $= \dfrac{\text{Number of mls. in concentrated sample}}{45}$

The formula for calculating the number of organisms per liter of water by the centrifuge-Rafter cell method is:

Organisms per liter of water = (Average number of organisms per ml. of concentrated sample) × (mls. in concentrated sample) × (number of centrifuged samples in one liter)

$$\text{Average number of organisms per ml. of concentrated sample} = \left( \frac{\text{Total organisms counted}}{\text{areas counted}} \right) \times \begin{array}{l}\text{(areas in}\\\text{Rafter cell)}\end{array}$$

$$\text{Number of centrifuged samples in one liter of water} = \frac{1000}{\text{mls. centrifuged}}$$

Throughout the investigation a varying number of areas from each sample was counted to determine the average number of organisms per area. This is discussed below in detail.

Biometrical methods used in interpreting the numerical facts of distribution and occurrence which have accrued from this study are not predominantly theoretical but rather practical and, it is hoped, are conducive to rational interpretation of the facts as they have been found to exist. A need is felt for a statistically sound basis upon which to state that the numerical results may be duplicated or if repeated would fall within a range that would not endanger the validity of a pre-determined conclusion. The procedures used are in keeping with standard methods of biometrical analysis and it is hoped will help to clarify the haze that often seems to enshroud plankton discussions. The several steps are considered separately or at least partly so, and efforts have been pointed in the direction of uniformity in so far as this is consistent with current practices.

## RESULTS

*Validity of Plankton Methods.*—Despite the large numbers of plankton samples studied in limnological as well as oceanographic investigations, there is a paucity of detailed information bearing on the precision that may be attributed to the several successive steps taken in the counting procedure. For this reason, an effort has been made to evaluate several sources of possible error in one method

and thereby indicate a basis for greater accuracy and a better understanding of the inherent limitations which the data possess.

The following points have been analyzed: (1) distribution of the areas counted in the Sedgewick-Rafter cell; (2) the relationship between the number of organisms present and the number of areas of the Rafter cell that must be counted in order to provide reproducible results; (3) the number of Rafter cells that should be counted; (4) the extent to which one centrifuge (volume, 350 ml.) or plankton trap sample (volume, 45 liters) may be considered typical for a specified location at a definite time; (5) comparison of the accuracy of the Foerst electric and the clinical centrifuges; and (6) validity of counts based on plankton trap samples.

It is pointed out that in general population analyses the main problem is to evaluate and reduce the *error of random sampling*. The samples selected for counting in the several steps considered may be regarded as representative. They have been selected at random and all organisms included had an equal opportunity of being selected. The sample differences may thus be attributed to errors of random sampling. In collecting plankton samples, and in the several steps necessary for the final preparation for counting, care must be exercised to rule out other errors. In analyzing the data for variance it is expected that variation may be due to random sampling and also to degree of clumping of organisms.

TABLE I.  *Variation in actual numbers due to method used in selecting groups of areas for counting on the Sedgewick-Rafter cell.  Magnification ×100, vol. 10 cmm.*

| Groups | Selection by random | Selection by rule |
|---|---|---|
| 1 | 28 | 22 |
| 2 | 39 | 27 |
| 3 | 32 | 37 |
| 4 | 24 | 39 |
| 5 | 28 | 38 |
| 6 | 22 | 38 |
| 7 | 39 | 37 |
| 8 | 42 | 31 |
| 9 | 27 | 22 |
| 10 | 28 | 29 |
| Mean | 30.9 ±1.46[1] | 32.0 ±1.45 |
| S.D. | 6.85±1.03 | 6.79±1.02 |
| Q. | 6.00 | 5.55 |
| $\frac{S.D.^2}{m}$ | 1.52 | 1.44 |

[1] Probable error.

The variance due to clumping would expectedly decrease accompanying increase in number of areas counted *i.e.,* volume of sample. There is not homogeneity of material as is indicated by $\sigma^2/m$ which would approach unity if material is homogeneous. The approach to unity is in the direction of 50 areas. This source of error could probably be overcome by further extending the counts—a rather impractical procedure. The percentage deviation from the mean, given in the tables, provides a satisfactory gross index of the reduced error accompanying increase in volume counted. To afford a basis for interpreting the reliance that can be placed in any single count based on volume and population intensities included in the tables, $Q$, the *quartile deviation,* or the semi-interquartile range, has been calculated. This statistic may prove most helpful in plankton work since it is based on frequency of variates rather than individual deviation magnitudes.

1. *Distribution of the Areas Counted in the Sedgewick-Rafter Cell.*—Areas for counting on the Sedgewick-Rafter cell have been determined by the method of random selection and also by following a specific rule designed to give each successive group of ten areas counted a relatively uniform distribution over the field

TABLE II.  *Variation in ten successive counts of 10, 20, 30, 40, and 50 areas on the same Sedgewick-Rafter cell.  Magnification ×210.  Population density—about 1800 per ml.*

| Group | 10 areas vol. 4.8 cmm. | | 20 areas vol. 9.6 cmm. | | 30 areas vol. 14.4 cmm. | | 40 areas vol. 19.2 cmm. | | 50 areas vol. 24 cmm. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean |
| 1 | 1633 | 6.95 | 2097 | 10.78 | 1909 | 7.31 | 1909 | 6.82 | 1962 | 7.68 |
| 2 | 2566 | 46.21 | 1722 | 9.03 | 1831 | 2.92 | 1635 | 8.50 | 1555 | 14.65 |
| 3 | 1541 | 12.19 | 1797 | 5.07 | 1623 | 8.76 | 2036 | 13.93 | 1700 | 6.69 |
| 4 | 1908 | 8.72 | 1473 | 22.19 | 1994 | 12.08 | 1760 | 1.51 | 1695 | 6.97 |
| 5 | 2141 | 21.99 | 1672 | 11.67 | 1859 | 4.50 | 1864 | 4.31 | 1805 | 0.93 |
| 6 | 1458 | 16.92 | 3051 | 16.16 | 1848 | 3.87 | 1583 | 11.41 | 1927 | 5.76 |
| 7 | 1958 | 11.56 | 2022 | 6.81 | 1465 | 17.65 | 1572 | 12.03 | 1860 | 2.09 |
| 8 | 991 | 43.53 | 1706 | 9.88 | 1443 | 18.88 | 1818 | 1.73 | 1992 | 9.33 |
| 9 | 1933 | 10.14 | 1460 | 22.87 | 1939 | 8.99 | 1820 | 1.85 | 1827 | 0.27 |
| 10 | 1416 | 19.21 | 1926 | 1.74 | 1884 | 5.90 | 1874 | 44.87 | 1899 | 4.23 |
| Total | 17545 | 197.42 | 18926 | 161.21 | 17795 | 90.86 | 17871 | 66.96 | 18222 | 58.60 |
| Mean | 1755 | 19.74 | 1893 | 16.12 | 1799 | 9.09 | 1787 | 6.70 | 1822 | 5.86 |
| P.E.$_m$ | 94.06 | 3.00 | 97.65 | 3.67 | 42.03 | 1.18 | 32.12 | 0.98 | 29.27 | 0.92 |
| S.D. | 441.02 | 14.06 | 457.83 | 17.21 | 197.04 | 5.55 | 150.59 | 4.59 | 137.24 | 4.31 |
| P.E.$_{S.D.}$ | 66.51 | 2.12 | 69.05 | 2.59 | 29.72 | 0.84 | 22.71 | 0.69 | 20.70 | 0.65 |
| Q. | 250.00 | 14.25 | 175.00 | 9.25 | 143.00 | 8.03 | 119.50 | 6.69 | 113.50 | 6.23 |

(table I). The results obtained by these methods are very similar.

These data are actual counts and not calculated numbers per liter of sample as is used hereafter in expressing quantities of organisms present. The fact that calculated numbers are given in the succeeding tables in no way modifies the interpretations that their statistics make possible except in so far as they bear upon the relation between means and variances of discrete data.

2. *The Relationship between the Number of Organisms and the Number of Areas (Volume of Sample) to be Counted.*—The numerical treatment of plankton samples is, in many respects, clearly a function of population density. The samples studied have been considered under four categories—those having numbers of about 1800 per ml., those ranging around 550 per ml., those around 140 per

ml., and also numbers varying around 90 per ml. The total quantity present throughout the year usually falls into one of these groupings. Considering the largest group first, it is shown in table II that the average of the percentage deviation from the mean is approximately 20, and $Q = 14$ when 10 areas of the Rafter cell—volume 4.80 cmm.—are counted. By trebling the number of areas counted, these statistics are reduced about 50 per cent. To further increase the volume counted results in but little improvement since counting 50 areas—volume 24 cmm. —only reduces the percentage deviation from 9 to 6 (figs. 1 and 2).

The data based on an intermediate population ranging around 550 per ml. show that the numerical reduction does not greatly decrease the reliability of the estimation (table III). Counting 40 areas— volume 19.2 cmm.—appears to give about
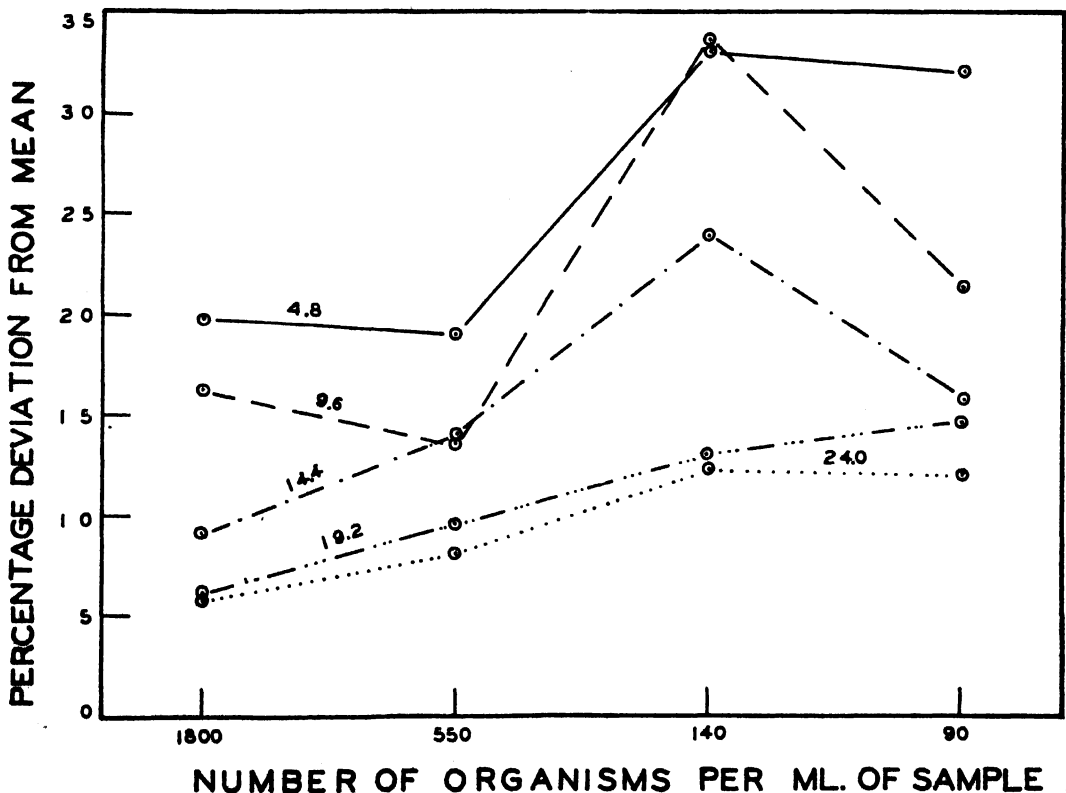


Fig. 1. Showing relationship between plankton density and volume of sample to be counted in Sedgewick-Rafter cell in order to assure different degrees of precision. Volume expressed in cmm.
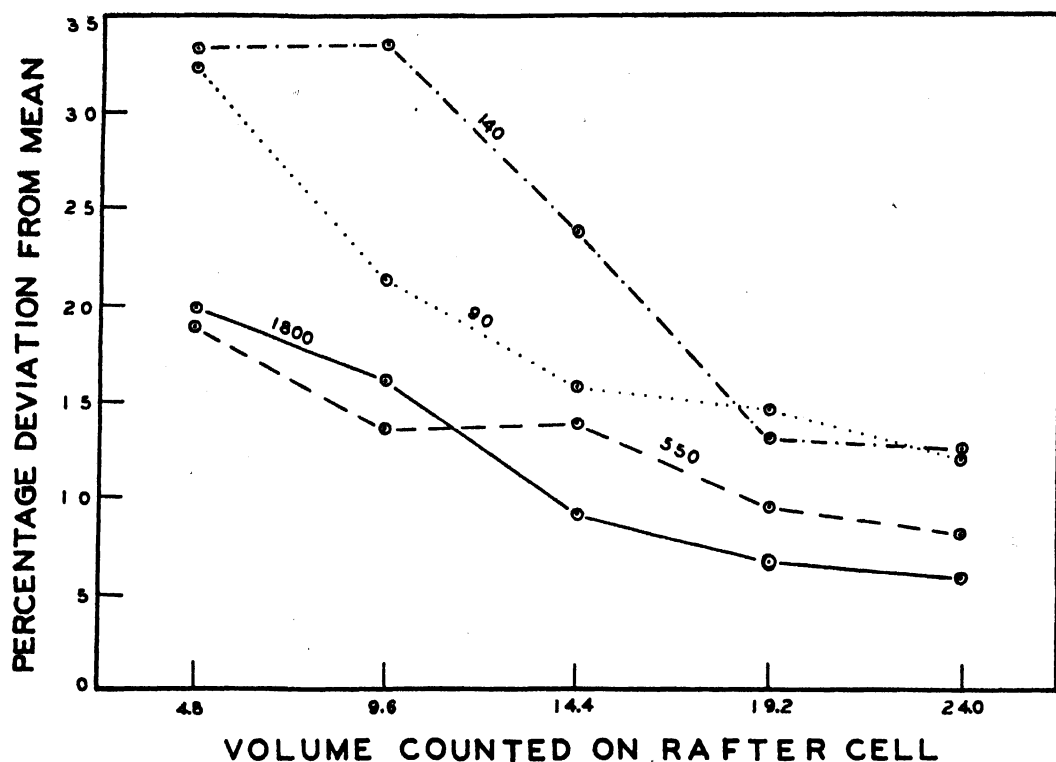
FIG. 2. Showing relationship between volume of sample counted in Sedgewick-Rafter cell and accuracy obtained. The concentration of plankton organisms is expressed in number per ml.

the same precision as by counting 30 areas —volume 14.4 cmm.—when 1000 or more organisms are present. Furthermore, the data suggest that reasonably accurate results may be obtained by counting 40 areas (fig. 1).

The counts of samples containing less than 500 organisms per ml. are expectedly far less dependable. As is shown in tables IV and V, a deviation of 21-34 per cent may be expected from estimations based on as many as 20 areas—volume 9.6 cmm.—when the population is around 100 per ml. It is seen that Q

TABLE III. *Variation in ten successive counts of 10, 20, 30, 40 and 50 areas on the same Sedgewick-Rafter cell. Magnification ×210. Population density—about 550 per ml; n = 10*

| Statistics | 10 areas vol. 4.8 cmm. | | 20 areas vol. 9.6 cmm. | | 30 areas vol. 14.4 cmm. | | 40 areas vol. 19.2 cmm. | | 50 areas vol. 24.0 cmm. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean |
| Mean | 554 | 18.93 | 542 | 13.67 | 534 | 13.91 | 551 | 9.54 | 547 | 8.15 |
| P.E.$_m$ | 25.99 | 1.96 | 20.69 | 2.26 | 18.24 | 1.38 | 12.94 | 0.95 | 11.66 | 1.09 |
| S.D. | 121.84 | 9.23 | 97.02 | 10.61 | 85.52 | 6.46 | 60.65 | 4.46 | 54.67 | 5.10 |
| P.E.$_{s.d.}$ | 18.38 | 1.39 | 14.63 | 1.60 | 12.90 | 0.97 | 9.15 | 0.67 | 8.25 | 0.77 |
| Q. | 79.00 | 14.26 | 79.00 | 14.57 | 66.50 | 12.46 | 46.50 | 8.43 | 48.00 | 8.77 |

TABLE IV.   *Variation in ten successive counts of 10, 20, 30, 40, and 50 areas on the same Sedgewick-Rafter cell.   Magnification ×210.   Population density—about 140 per ml.; n = 10*

| Statistics | 10 areas vol. 4.8 cmm. | | 20 areas vol. 9.6 cmm. | | 30 areas vol. 14.4 cmm. | | 40 areas vol. 19.2 cmm. | | 50 areas vol. 24.0 cmm. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean |
| Mean | 128 | 33.38 | 145 | 33.67 | 135 | 23.99 | 139 | 13.08 | 147 | 12.40 |
| P.E.$_m$ | 11.09 | 4.38 | 12.30 | 3.86 | 8.60 | 3.36 | 5.09 | 2.19 | 5.02 | 1.98 |
| S.D. | 51.99 | 20.53 | 57.68 | 18.08 | 40.33 | 15.74 | 23.86 | 10.26 | 23.52 | 9.27 |
| P.E.$_{S.D.}$ | 7.84 | 3.10 | 8.70 | 2.73 | 6.08 | 2.37 | 3.60 | 1.55 | 3.55 | 1.40 |
| Q. | 33.50 | 26.?5 | 41.50 | 28.66 | 28.00 | 20.68 | 17.50 | 12.61 | 16.50 | 11.24 |

TABLE V.   *Variation in ten successive counts of 10, 20, 30, 40, and 50 areas on the same Sedgewick-Rafter cell.   Magnification ×210.   Population density—about 90 per ml.*

| Group | 10 areas vol. 4.8 cmm. | | 20 areas vol. 9.6 cmm. | | 30 areas vol. 14.4 cmm. | | 40 areas vol. 19.2 cmm. | | 50 areas vol. 24.0 cmm. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean |
| 1 | 93 | 2.2 | 67 | 21.2 | 76 | 12.2 | 87 | 3.8 | 99 | 6.3 |
| 2 | 46 | 51.6 | 108 | 26.9 | 80 | 7.6 | 93 | 10.9 | 74 | 20.5 |
| 3 | 139 | 46.2 | 114 | 34.0 | 99 | 14.3 | 78 | 6.9 | 97 | 4.2 |
| 4 | 128 | 34.6 | 73 | 14.2 | 87 | 0.5 | 70 | 16.4 | 115 | 23.5 |
| 5 | 139 | 46.2 | 110 | 41.0 | 108 | 24.7 | 109 | 30.1 | 101 | 8.5 |
| 6 | 93 | 2.2 | 67 | 21.3 | 104 | 20.1 | 95 | 13.4 | 106 | 13.8 |
| 7 | 128 | 34.6 | 78 | 8.3 | 69 | 20.3 | 59 | 29.5 | 97 | 4.2 |
| 8 | 23 | 75.8 | 89 | 4.6 | 87 | 0.5 | 90 | 7.4 | 90 | 3.3 |
| 9 | 93 | 2.2 | 72 | 15.4 | 103 | 18.9 | 67 | 20.0 | 81 | 12.9 |
| 10 | 69 | 27.4 | 63 | 26.0 | 53 | 38.7 | 90 | 7.4 | 71 | 23.7 |
| Total | 951 | 323.0 | 851 | 212.9 | 866 | 157.8 | 838 | 145.8 | 931 | 120.9 |
| Mean | 95.1 | 32.30 | 85.1 | 21.29 | 86.6 | 15.78 | 83.8 | 14.58 | 93.1 | 12.09 |
| P.E.$_m$ | 8.51 | 5.22 | 4.56 | 2.40 | 3.75 | 2.46 | 3.22 | 2.00 | 3.00 | 1.85 |
| S.D. | 37.85 | 23.24 | 20.26 | 10.66 | 16.66 | 10.96 | 14.33 | 8.88 | 13.35 | 8.23 |
| P.E.$_{S.D.}$ | 6.02 | 3.69 | 3.22 | 1.69 | 2.65 | 1.74 | 2.28 | 1.41 | 2.12 | 1.31 |
| Q. | 29.50 | 31.02 | 20.50 | 24.09 | 13.50 | 15.59 | 10.00 | 11.93 | 10.00 | 10.74 |

may be as high as 28 per cent when 20 areas are counted. Doubling this number of areas only reduces the quartile deviation to 12 per cent. At least 40 and preferably 50 areas—volume 24.0 cmm.—should be counted to reduce the expected percentage deviation to as low as 13 per cent.

### 3. Number of Rafter Cells that should be Counted.

—In order to provide an expression of the variation in the number of organisms in successive 1 ml. samples of the concentrate obtained by centrifuging a single 350 ml. water sample, data are presented for each of four water samples, which were counted seven times. They were counted in the following manner. After centrifuging for four minutes, a 1

TABLE VI.   *Variation between individual Rafter cells counted from the concentrates of four 350 ml. water samples.   Number of areas counted in each Rafter cell, 40 (volume 19.2 cmm.)*

| Rafter cell No. | Concentrate No. 1 | | Concentrate No. 2 | | Concentrate No. 3 | | Concentrate No. 4 | |
|---|---|---|---|---|---|---|---|---|
| | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean | Calc. no. | Per cent deviation from mean |
| 1 | 629 | 9.52 | 589 | 7.21 | 474 | 2.09 | 526 | 9.78 |
| 2 | 503 | 12.42 | 651 | 18.49 | 543 | 12.17 | 549 | 14.59 |
| 3 | 594 | 3.43 | 526 | 4.26 | 520 | 7.42 | 457 | 4.61 |
| 4 | 577 | 0.47 | 543 | 1.16 | 497 | 2.66 | 474 | 1.06 |
| 5 | 577 | 0.47 | 491 | 10.63 | 257 | 46.91 | 440 | 12.33 |
| 6 | 601 | 4.65 | 429 | 21.91 | 549 | 13.41 | 354 | 26.11 |
| 7 | 539 | 6.15 | 617 | 12.30 | 549 | 13.41 | 554 | 15.63 |
| Total | 4020 | 37.11 | 3846 | 75.96 | 3389 | 98.07 | 3354 | 84.11 |
| Mean | 574.3 | 5.30 | 549.4 | 10.85 | 484.1 | 14.01 | 479.1 | 12.01 |
| S.D. | 41.59 | 4.46 | 76.44 | 7.45 | 104.22 | 15.28 | 71.33 | 8.15 |
| P.E.$_{s.D.}$ | 7.50 | 0.80 | 13.78 | 1.34 | 18.79 | 2.75 | 12.86 | 1.47 |
| P.E.$_m$ | 10.60 | 1.14 | 19.49 | 1.90 | 26.57 | 3.89 | 18.18 | 2.08 |
| Q. | 24.50 | 4.27 | 48.00 | 8.74 | 30.00 | 6.20 | 44.50 | 9.29 |

ml. sample of the concentrate was removed to the Rafter cell and 40 areas (volume 19.2 cmm.) were counted. Analysis of the data shows that the Rafter cells of each sample show a fairly good agreement, the percentage deviation being 5 and 14 per cent and the quartile deviation ranging from 4 to 9 per cent (table VI). It should be noted that these values represent average or less than average populations. In more heavily populated waters a still better agreement may be anticipated.

4. *The Extent to Which a Single Centrifuge or Plankton Trap Sample may be Considered Typical.*—To ascertain the representative character of a single centrifuge sample of about 350 ml., collections were made at close time intervals and the same procedure was followed in making the 14 counts (for each sample, 20 areas were counted in each of 3 Sedgewick-Rafter cells). Despite the fact that we cannot assume an absolutely uniform population in the water from which the samples were drawn due to the time interval being spread out over the period from 11:05 A.M.–2:55 P.M., nevertheless, the results show relatively small total varia-

tions, the mean being, in round numbers, 78631 ± 2210 (table VII).

In table VIII the results of four 350 ml. samples taken from a sample container automatically stirred, show the normal expectancy with respect to variation.

5. *Comparison of Counts Based on the Use of the Foerst and Clinical Centrifuges.*—A comparison of the Foerst cen-

TABLE VII.   *Surface variations in plankton populations at close time intervals based upon plankton trap samples for macroplankton and centrifuge samples for microplankton*

| Time | Organisms per liter | |
|---|---|---|
| | Macroplankton | Microplankton |
| 11:05 A.M. | 62 | 97,093 |
| 11:25 A.M. | 47 | 88,058 |
| 11:35 A.M. | 17 | 79,544 |
| 11:55 A.M. | 16 | 79,720 |
| 12:05 P.M. | 67 | 76,300 |
| 12:13 P.M. | 64 | 90,234 |
| 12:25 P.M. | 77 | 98,535 |
| 12:35 P.M. | 41 | 72,512 |
| 12:42 P.M. | 47 | 75,225 |
| 12:52 P.M. | 37 | 64,600 |
| 1:55 P.M. | 59 | 84,285 |
| 2:04 P.M. | 59 | 64,712 |
| 2:50 P.M. | 45 | 56,535 |
| 2:55 P.M. | 50 | 73,483 |
| Mean | 49.14±3.2 | 78,631.14±2,210.17 |
| S.D. | 17.00±2.2 | 12,261.01±1,562.91 |

TABLE VIII. *Showing variation in four 350 ml. samples taken from a single 30 liter volume thoroughly stirred*

| Sample No. | Mean number of organisms pr. ml. | Deviation from mean | Percentage deviation |
|---|---|---|---|
| 1 | 574.3 | 52.6 | 10.08 |
| 2 | 549.4 | 27.7 | 5.31 |
| 3 | 484.1 | 37.6 | 7.21 |
| 4 | 479.1 | 42.6 | 8.17 |
| Mean | 521.7 | 40.1 | 7.69 |

trifuge with the clinical electric centrifuge used by Gran was made by taking from the same samples two volumes, one of 340 ml. which was centrifuged in the usual manner by the Foerst centrifuge and one of 60 ml. which was placed in the four 15 ml. tubes of the second centrifuge that was operated at 2950 R.P.M. for thirty minutes. Twenty samples were studied in this manner, the results from which are presented in table IX. The data

TABLE IX. *Comparison of the efficiency of the Foerst and the four-tube centrifuges*

Samples above 500,000 organisms per liter

| Sample number | Foerst centrifuge | Four-tube centrifuge |
|---|---|---|
| 1 | 748,483 | 574,505 |
| 2 | 879,997 | 460,032 |
| 3 | 868,570 | 404,582 |
| 4 | 619,995 | 558,323 |
| 5 | 776,854 | 483,116 |
| 6 | 712,065 | 436,946 |
| 7 | 891,424 | 791,006 |
| 8 | 876,852 | 515,482 |
| 9 | 574,505 | 121,900 |
| 10 | 822,857 | 550,232 |
| Samples below 500,000 organisms per liter |  |  |
| 1 | 329,283 | 136,316 |
| 2 | 446,653 | 142,975 |
| 3 | 329,283 | 136,316 |
| 4 | 413,938 | 224,000 |
| 5 | 374,426 | 128,310 |
| 6 | 360,845 | 225,113 |
| 7 | 349,999 | 150,833 |
| 8 | 327,284 | 153,650 |
| 9 | 320,998 | 124,320 |
| 10 | 466,969 | 131,655 |

show conclusively that the clinical centrifuge thus operated yields results which are low by approximately 30 per cent.

6. *Validity of Counts Based on Plankton Trap Samples.*—Analyses of the data obtained by using the plankton trap for collection indicates that only about 2 per cent of the microplankton is retained (table X). This fraction is, expectedly,

TABLE X. *Comparison of plankton counts based on plankton trap-centrifuge samples[2] and Foerst centrifuge samples. Each count represents an average of three separate samples*

| Haul numbers | Plankton trap | Plankton trap-centrifuge | Foerst centrifuge |
|---|---|---|---|
| 6–10–15 | 1,423 | 122,243 | 88,232 |
| 20–25–26 | 1,699 | 64,375 | 82,085 |
| 27–28–29 | 1,664 | 88,355 | 81,757 |
| 30–31–32 | 1,162 | 56,135 | 71,199 |

[2] Obtained by centrifuging, with the Foerst centrifuge, water that had been strained through the plankton trap.

subject to variation, depending on the number of samples that have passed through the netting, thus tending to fill up the interstitial spaces of the net. This is shown by comparing the "plankton-trap-centrifuge" and the "Foerst centrifuge" columns in table X. These illustrations clearly indicate that the plankton trap can be depended on to retain only the macroplankton which includes principally the mature copepods and the larval stages with the exception of the first nauplius stage, rotifers, cirripede larvae and also such larger forms that are occasionally present in the plankton.

A series of plankton trap samples taken at the same place at close time intervals provides an indication of the representative character of data based on a single trap collection. In a series of 14 samples collected during a period 11:05 A.M.–2:55 P.M., the mean macroplankton count obtained was 49.1 ± 3.2 per liter. This provides a fairly good idea of the precision possessed by total counts of the larger plankton forms (table VII). In view of the pronounced hourly changes in macroplankton population that are known to take place it seems likely that a significant

part of the variation for the three hour period of collecting indicated in table VII, is due to actual differences in the number of organisms present and not entirely a result of the inaccuracy of the method of sampling. The possibility of error due to sampling variability must also be recognized.

In conclusion, it would seem that plankton densities much below 100,000 per liter are difficult to measure satisfactorily with the procedure outlined above unless relatively large water samples are centrifuged. One author has used the common clinical centrifuge and a volume of not over 100 ml. and reports total numbers of diatoms as low as 80 per liter. This means that the original sample contained less than $\frac{1}{10}$ of a diatom per ml. Furthermore, it means that the concentrate, obtained after centrifuging, having a volume probably not exceeding 10 ml., contained only 8 diatoms, a concentration of less than one organism per ml. of concentrate which is obviously too small a number to yield reliable estimations. In other words, it has been our experience that low counts are impossible to duplicate unless the standard procedure is modified. It appears that this may be accomplished by increasing the amount centrifuged. Such a step does, of necessity, increase the labor and time involved but yet it is practical while using the Foerst centrifuge. Thus, we obtained in table IV an actual count of 10 and a corresponding calculated number of 83 per ml. The former count represents the actual number of organisms in a volume of 4.8 cmm. of the concentrate which was transferred from the storage vial with a pipette to the Sedgewick-Rafter cell for counting purposes. It is the equivalent of 83,000 organisms per liter or 83 million per $m^3$. There is reason to believe that the number, 130, obtained by counting a volume of 24.0 cmm. is more correct. If 700 ml. of water had been centrifuged in place of 350 ml., we might expect 20 instead of 10 organisms in 4.8 cmm. or 156 instead of 78 on a basis of a 24.0 cmm. volume.

This would raise the standard of estimation to the level ordinarily obtained by counting water samples containing around one- million organisms per liter. In all instances, care must be exercised to count enough organisms to reduce sampling variations to a minimum.

During seasons of low plankton production or in certain types of field or laboratory experiments for which numerical data on individual species are desired, accuracy may be greatly improved by increasing the volume collected for centrifuging.

## DISCUSSION

There exists much diversity of opinion with regard to quantitative analyses of animal populations. Much may be said in favor of each method and likewise considerable condemnation may be and often is expressed. Unfortunately, such destructive criticism is frequently not without some justification. The observer, in many instances, cannot fail to be impressed by the total absence of a remedial procedure that will improve the status of current practices.

In considering the general problems involved, attention should be given to certain fundamental tenets that may furnish a logical background for the development of quantitative concepts of occurrence in time and space of a hypothetical population of organisms. Numerical distribution in time and space, of necessity, implies the element of chance and, therefore, the application of statistical ideas should prove constructive in formulating a picture of existing numbers in a certain location.

The following points may warrant consideration—(1) the modifying effect of environment in producing aggregations; (2) the ratio of the size to the number of organisms; (3) the relationship between the size of the organism and the availability of requisite food supply; (4) the normal range of migration characteristic of the organism; and (5) the reproductive potential of the organism. Such in-

formation in relation to a single organism or a group of organisms constitutes a basis for interpreting numerical concepts of distribution.

Plankton forms are, in general, short-lived, subject to the movement of water particles surrounding them and capable of a small degree of movement themselves, responsive to slight environmental change and closely bound in with the vital food chains of aquatic organisms. They represent a highly variable population with respect to time and their characteristics are perhaps better interpreted in light of the environmental conditions known to exist at the particular time and exact place of sampling. For this reason, it is highly desirable to be able to express quantitatively the planktonic characteristics of the water as well as the physical or chemical properties. Admittedly, the errors are too large even after most careful observation. To achieve a numerical expression of the range of expected error is not without purpose (Herdman, '23; Johnstone, Scott and Chadwick, '24).

The common quantitative procedures such as the pump method, the settling method, the pigment method, as well as others, are well known (Robert, '22; Allen, '30; Harvey, '34). Their application for several well-defined purposes is in no way questioned. Harvey ('34) aptly expresses the opinions of many when he states "the only strictly quantitative method of sampling the population is to centrifuge a small sample of water and count the plants in it." The importance of establishing a definite purpose and then using a technic of sampling and counting best fitted to suit that purpose is well brought out by Professor Allen in his illuminating treatment of this subject (Allen, '34). The present results are presented not with the idea of establishing conclusively the points developed on quantitative estimations of numbers but rather to add to the existing data bearing on this subject and possibly to stimulate in others an interest in the more strictly quantitative phases of planktonic analyses.

It has been found that counts based upon the selection of groups of areas at random are about the same as those obtained according to selection by rule (table I). In the process of counting, it has been observed that the heavier forms show a slight tendency to settle and collect along the edges of the Rafter cell. There is also a clumping of forms in the Rafter cell that has been observed. This introduces an additional error, the magnitude of which will depend on the number of areas counted.

The precision obtained in plankton counts is largely a function of population density and the volume counted (fig. 1). The dependability of the counts obtained by the use of different volumes of sample material is indicated by a close examination of tables 2–5. The application of these findings is not necessarily limited to total counts on the Rafter cell. They may be used as an index of the number of individual organisms that should be considered when treating the separate components of a plankton collection. The several statistics should be employed as a basis for analyzing significant differences in space and time variations. In this connection the quartile deviation, $Q$, becomes an exceedingly useful statistic in that it indicates the distance from the median within which half the individual counts are likely to fall. The degree of variance, $\sigma^2/m$, may be expected to decrease with increase of volume counted, thus indicating an approach to homogeneity. This approach is expectedly more rapid in the more dense populations.

However, variance is considered to be due chiefly to two factors—errors of random sampling and errors caused by clumping in the counting cell. The problem of separating these two and interpreting their respective significance in affecting counts is a somewhat difficult one. We believe it may be approached in the following way. Let $p$ represent the relative volume occupied by organisms, $q$ or $1 - p$ represent the relative volume free of organisms and let $N$ be a function

of the volume used. The mean should equal $Np$ and the variance $Npq$. In dilute solutions $q$ should approach 1 and the resulting distribution should approach a Poisson series in which the variance (standard deviation squared) equals the mean, provided that the sample is homogeneous. Therefore, any value for variance in excess of the mean should give evidence of heterogeneity which on the basis of observations is attributed to clumping. Our calculations of more concentrated solutions indicate that $q$ is in excess of 0.985. At present an effort is being made to evaluate the relative importance of these two sources of error. The two factors—errors of random sampling and errors of clumping—are not considered to respond similarly to numerical variations in the samples. In a small concentration there may not be enough material for clumping hence error may be attributed mainly to small numbers. Granting there are enough organisms present to permit clumping, there is likely to be a rapidly increasing error followed by a gradual decrease until sufficient areas are counted to average out this source of error. At the beginning of clumping a large error is expected due to clumping and due to random sampling. At this point the former is increasing and the latter decreasing with increase in number of organisms present. At a point on the curve at which insufficient numbers are present to produce clumping, the variance is due to errors of random sampling. Thus it appears that we are dealing with two errors that theoretically may be represented by curves of very different slopes when plotted against population numbers. Herein may lie the explanation for the divergence shown in figure 2 (upper two curves). The analysis for variance in any practical consideration is further complicated by need for exercising care in deciding on the approximate volume of samples to be counted in order to yield comparable results from samples of variable population intensity.

The numerical treatment of plankton populations exceeding 500,000 per liter should offer little difficulty when once consistent methods of counting and handling the sample have been worked out. When this and larger numbers are present, the volume used may be reduced to 14.4 cmm. and in some instances to 9.60 cmm. providing the particular purpose of the data does not demand a high degree of accuracy. Cognizance must be taken of the fact that there is always a possible range of error accompanying the process of sampling and preserving so that a need is felt for taking precautions in the more mechanical aspects of the process to parallel the accuracy gained from proper biometrical treatment of the problem.

It is exceedingly difficult to secure counts that may be duplicated when the number falls much below 100 per ml. Numerous estimations have been made which serve only to prove that the results are not convincing unless a volume of impracticable proportions is counted. For samples ranging around 100 per ml., a volume of at least 19.2 cmm. should be used (tables IV and V). Harvey, Cooper, Labour, and Russell ('35) used a volume of 0.194 cc. usually from about one-fifth of a liter of sea water, for estimating total numbers of diatoms and dinoflagellates in samples containing upwards of 15,000 per liter. It would seem that when counts are to be made of large numbers of species, the quantity of water centrifuged should be such as to give numbers of individual species in the concentrate sufficient to reduce the probable error of random sampling to insignificance.

Mention has been made of the possible error due to the sampling of one ml. of the concentrate. Thorough shaking of the concentrate which usually has a volume of about 10–15 ml. fails to give a uniform distribution as indicated by the removal of 1 ml. aliquots for use in the Sedgewick-Rafter counting cell. However, the variation is not sufficiently great to necessitate the use of more than one

ml. sample in conducting routine estimations (table VI).

The value of the data on microplankton presented in table VII is lessened because of the two inherent variables to which they are subject—namely, time variation and variation due to sampling. However, several of the time intervals are sufficiently small to warrant the assumption that the water contained a fairly uniform population. Granting this, then the variation in counts may be attributed, in the main, to sampling differences. The variability seems low enough to warrant the use of a 350 ml. volume of water for sampling purposes when the number is around 500,000 per liter. This point is confirmed by the data presented in table VIII. The average percentage deviation from the mean of four samples taken under ideal conditions is about 8. Again, the desirability of collecting a *large* sample for centrifuging is clearly recognized, especially during seasons of low plankton production.

The need for exercising care in the process of centrifuging is clearly brought out by the results in table IX. The Foerst centrifuge permits using any desired quantity of water whereas the ordinary clinical centrifuge is more limited in this respect. It has been possible to demonstrate the high degree of efficiency of the Foerst centrifuge as previously described (p. 310). The inefficiency of the clinical centrifuge, as indicated by the reduction in numbers of approximately 30 per cent, may possibly be caused by the smaller volume of water centrifuged or more likely by incomplete removal of the plankton. In attempting to use this type of centrifuge for quantitative work, it is necessary to test out these two points in order that desired accuracy be assured.

The current usage of the Foerst plankton trap has led to certain experimental procedures designed to show its degree of dependability for micro- and macroplankton sampling. Obviously, the type of net employed will determine the size of the organisms collected. In this work a number 20 net, having 187 meshes to the inch was employed. The small percentage—namely, 2 per cent—of microplankton retained speaks for itself. With constant usage, this percentage does increase, since the interstitial spaces in the net become partially filled with organisms as well as detritus. That the plankton trap is a reliable instrument for sampling macroplankton forms may be easily demonstrated. The results of successive macroplankton samples presented in table VII give a fairly good idea of the representative character of a single sample. The standard deviation is admittedly high. However, it is seen that the period of sampling was quite long, thereby introducing the possibility for considerable variation in the numbers of forms actually present in the water at the time of sampling. Until greater accuracy has been demonstrated for another instrument designed for macroplankton analysis, it is believed that many current problems may be solved through the use of this sampling device.

SUMMARY

Quantitative plankton experiments have been conducted for the purpose of evaluating the magnitude of error in the several steps of the methods used. Samples have been taken using a 350 ml. water bottle and the Foerst plankton trap. The Foerst electric centrifuge and the common clinical centrifuge were used and the Sedgewick-Rafter cell employed for numerical estimations.

The experiments were designed to determine the variation due to distribution of areas counted in the Rafter cell, the relation between the number of organisms in the sample and the volume that should be counted, the number of Rafter cells to be counted, the representative character of a single centrifuge or plankton trap sample, the efficiency of the Foerst centrifuge as compared with the clinical centrifuge and the validity of counts based on the plankton trap samples.

Variance obtained in counts made on

the above basis is attributed mainly to two factors—errors of random sampling and errors of clumping. It is important to estimate the magnitude of these two factors and thus provide a guide for critical numerical analyses.

Evidence has been presented to show the necessity for centrifuging a sufficient quantity of water to give numbers of selected organisms in the concentrate large enough to reduce the errors to insignificance.

Numerous observations are reported bearing on these several points and the results are graphed and tabulated so as to show in part the extent to which quantitative plankton estimations, obtained according to the stated procedure, may be used for interpretive purposes.

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# NORMAL GROWTH AND DEVELOPMENT OF SOUTHERN PINE SEEDLINGS IN THE NURSERY

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## INTRODUCTION

Records of *normal* seedling behavior and seedbed conditions, by providing the basis for comparison with *abnormal* behavior and conditions, would help seedling growers to detect departures caused by injury from diseases or insects, experimental treatment, or accidental causes. Recognizing these departures, growers then can modify their practices so as to produce better seedlings at a lower cost.

The present study, therefore, was designed to provide a measure of (1) normal seedling growth and development and (2) the conditions under which this occurred. Specifically, this included (1) top length, stem diameter, root length, and root extent [2] of longleaf (*Pinus palustris*), slash (*P. caribaea*), loblolly (*P. taeda*), and shortleaf (*P. echinata*) pine seedlings, and (2) temperature and moisture content of air and soil in the nursery bed from the time the seed was sown until the seedlings were lifted for field planting.

## LITERATURE

In surveying the literature on normal development of plants, it is interesting to note that researches dealing with root

[2] An index of root extent is obtained by adding together the lengths of all rootlets over 2 cm. long as measured from the ground line to the tips. The index thus represents the total length of the absorbing roots of the seedling. The method of computing this index is described by Huberman, M. A., in *Occasional Paper* No. 44, Southern Forest Experiment Station, March 20, 1935.

growth and competition are voluminous, those treating of the normal development of tree species are comparatively few, and those dealing with tree-seedling growth in the nursery are even fewer.

The papers of Stevens ('31) and Laing ('32) are perhaps the most pertinent. In the report of his study of the root growth of white pine, Stevens cited the results of European workers from du Monceau in 1760 to Magyar in 1929, and of American workers from Cannon in 1914 to Holch in 1931. In general, these workers agree more or less closely that (1) during the growing season there are two periods of root activity, one in the spring and the other in late fall; (2) rate of growth is difficult to correlate with weather or soil conditions; (3) changes in the rate of development during the growing season are due to internal causes or to a complex combination of environmental factors; (4) that *total* annual growth varies with soil conditions.

Laing (1932), in a careful study of tree roots in Great Britain, found that in the case of *Picea excelsa, P. sitchensis,* and *Larix europaea,* (1) there was no appreciable root growth during the winter months; (2) shoot growth (with second-year seedlings) commenced first in the spring and was followed by root elongation, and throughout the season thereafter there was an interplay between root and shoot development; (3) in the latter part of the year, after shoot growth had ceased, the root activity continued. He suggested, quite logically, that the shoot grew until the root was no longer able to supply the greater transpiring surface created by the new leaves, when new root extension was required, and he confirmed this interplay of root and shoot growth by weight determinations and by observing the variations in top-root ratios.

## The Study

In 1934 plots of longleaf and slash pines were sown about the middle of April; in 1935, plots of longleaf, slash, and shortleaf pines were sown about the middle of March; and in 1936, plots of longleaf, slash, shortleaf, and loblolly pines were sown about the first week in March at the Stuart Forest Nursery in central Louisiana. The plots consisted of standard nursery beds, which were drill-sown and cared for in accordance with regular nursery practice. In 1935 and 1936, for each species detailed records of germination, seed loss, seedling establishment, and final production were made on 20 drills of exactly 100 seeds each. Late in May the beds were thinned to uniform density, and a count was made of the number of trees removed. At the end of the season, the seedlings were graded, and a record kept of the number of culls. From the remaining portion of the beds, samples of 30 complete seedlings were dug up at 10-, 20-, or 30-day intervals. The root length, root extent, stem diameter, and top length of these seedlings were measured; top lengths were taken to the tip of the cotyledons, to the tip of the primary needles, to the growing point, and in the case of longleaf pines to the tip of the secondary needles, according to the stage of development. In 1936 dry weights of tops and roots were determined separately, and top-root ratios were computed for each periodic sample. However, since the top-root ratios failed to reveal anything striking, they are not discussed further.

Descriptive notes of the various growth activities, such as emergence and development of primary and secondary needles, bark formation, and appearance of mycorrhizae, were kept throughout the season. Photographs were also taken periodically.

In 1936 records were kept of precipitation and of maximum and minimum air temperatures at the Cooperative Weather Station at the Nursery, of soil temperatures at the surface and at several depths, of air temperature, relative humidity, and evaporation from black and white atmometers in the seed beds, and of soil moisture in the root zone.

The germination records and the measurements of the seedlings and of the growing conditions were analyzed, and the tabulated results are presented here. No attempt was made to correlate growth rate with weather or site factors because (1) the study was not designed to show this, and (2) attempts at such correlation by other workers have given such little promise. The accompanying tables and graphs, however, provide a fairly complete picture of the growing conditions in the seed beds.

## Results and Discussion
### Germination

After the seeds had been in contact with the soil for 12 to 20 days and had imbibed sufficient moisture, the first evidence of activity was the horizontal emergence from the partially split seed coat of the radicle with its slimy protective sheath. Within a day or two, depending on weather conditions, the tip turned downward and came in contact with the soil particles. If not disturbed by wind or beating rain, the tip then pushed between the particles, became firmly anchored, and began functioning as a root.

While the root tip was being established, the cotyledons of the longleaf pine —and the stem and cotyledons of the slash, loblolly, and shortleaf pines—elongated and straightened up, lifting the seed coat into the air. When the cotyledons had fully developed, they bent outward near their middle, gradually forcing off the seed coat, which finally (sometimes aided by wind movement or disturbance by rain) dropped off, permitting them to open out into a rosette, in the center of which were the rudimentary primary needles. In longleaf pine, the base of this rosette was just above the ground level; in shortleaf, loblolly, and slash pines, a short stem supported the rosette.

TABLE I.   *Course of germination, establishment, and development,
expressed as percentages of total seed sown, 1936*

| Species | Laboratory germination[1] | Seed bed germination[2] | Loss after germination by principal causes | | | | | | | Failed to germinate | Total living | Removed in thinning | Culled at lifting | Plantable |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Failed to root | Damped off | Insects | Heat | Mechanical | Unknown | Total | | | | | |
| Lglf. | 46.8 | 45.9 | 8.4 | 0.8 | 0.0 | 0.0 | 0.1 | 0.8 | 10.1 | 54.1 | 35.8 | 20.0 | 3.7 | 12.1 |
| Slash | 75.2 | 68.9 | 3.3 | 2.1 | 0.0 | 0.0 | 4.9 | 1.2 | 11.5 | 31.1 | 57.4 | 33.2 | 6.5 | 17.7 |
| Lob. | 34.0 | 39.2 | 8.5 | 1.0 | 0.0 | 0.0 | 0.5 | 1.0 | 11.0 | 60.8 | 28.2 | 10.2 | 1.4 | 16.6 |
| Shtlf. | 62.4 | 47.3 | 1.1 | 1.2 | 0.0 | 0.0 | 1.0 | 1.8 | 5.1 | 52.7 | 42.2 | 21.6 | 3.9 | 16.7 |

[1] Based on tests of 250 seeds set up in sand flats on same day as seeds sown in nursery; at end of 45 days.

[2] Based on 2000 seeds of each species; all values to the right of the first column refer to nursery bed results.

Among the various causes of loss following germination (table I), failure to take root appeared most common. Wind or lifting the burlap just after the emergence of the radicle often forced the tip of the radicle out of contact with the soil and exposed it to drying. Once this tip dried, the seedling seldom took root, and recovery was unusual. Loss from damping-off, insects, or heat was practically absent. When lifting the burlap was delayed too long, mechanical breakage oc-
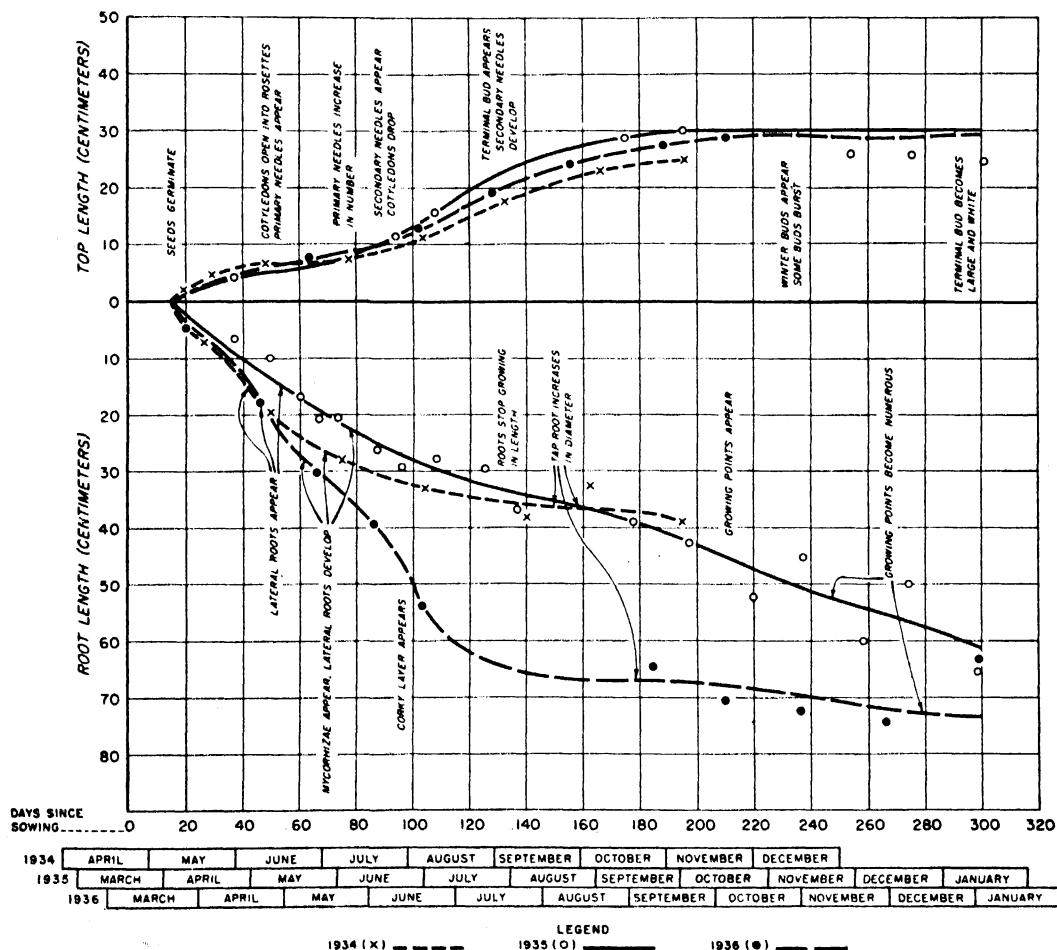


FIG. 1.   Cumulative growth of tops and roots—longleaf pine.

curred in a few instances. Birds accounted for the loss of a very few seedlings by pulling off the seed coat before the cotyledons had fully developed.

The losses following germination were relatively unimportant as compared with those due to non-viable seed. Furthermore, the fact that nursery germination was about as good as the laboratory germination indicates that loss in viability was not due to conditions in the nursery.

### Growth

During and immediately following the establishment of the seedlings, 15 to 45 days after sowing, the root elongated rapidly (figs. 1–4, 6–7). At the same time the cotyledons opened and the primary needles began to form and elongate. For the next 30 to 40 days (the latter part of May until the middle of July) elongation of the primary root continued rapidly; secondary or lateral roots and

mycorrhizae appeared, a corky layer formed on most of the roots, primary needles increased in size and number, and secondary needles appeared. During the next 45 to 90 days (fig. 8) (July–September) primary-root elongation practically ceased, root-crown diameter and stem diameter began to increase, secondary needles increased in length and number, and in slash, loblolly, and shortleaf pines the stems increased in length. Toward the end of this period the terminal bud appeared. Bark formed on the stems of slash, loblolly, and shortleaf. Mycorrhizae were abundant.

From September 1 (fig. 9) until about the middle of October the chief activity was bud formation and development. Slash pine, and especially loblolly and shortleaf pines, exhibit the multinodal character even in their first year in the nursery. The nodal buds appeared in slash pine 160 to 190 days after sowing
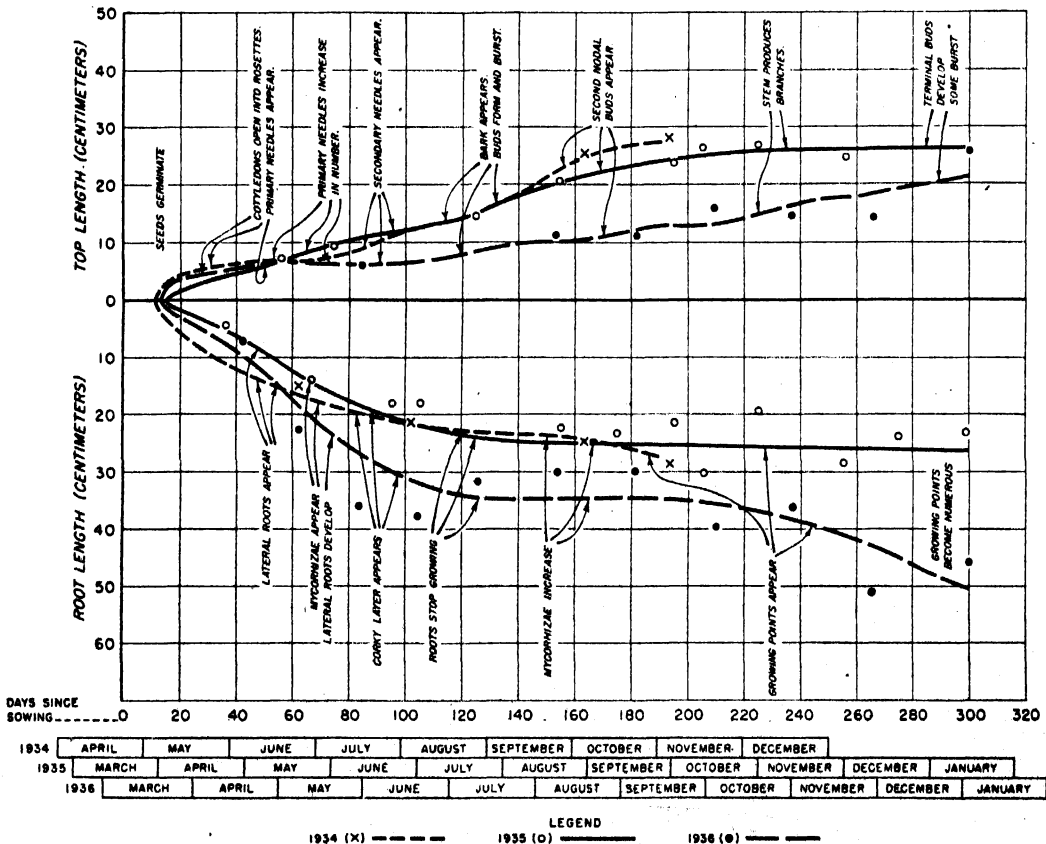


FIG. 2. Cumulative growth of tops and roots—slash pine.
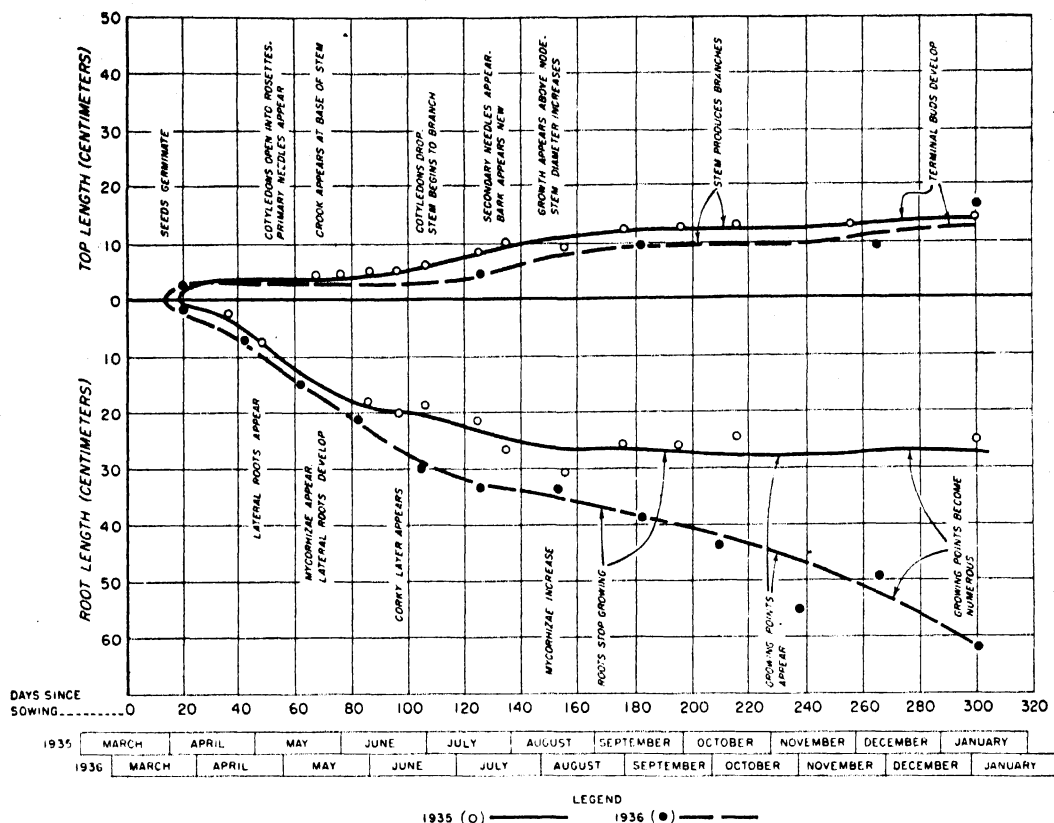
FIG. 3.   Cumulative growth of tops and roots—shortleaf pine.
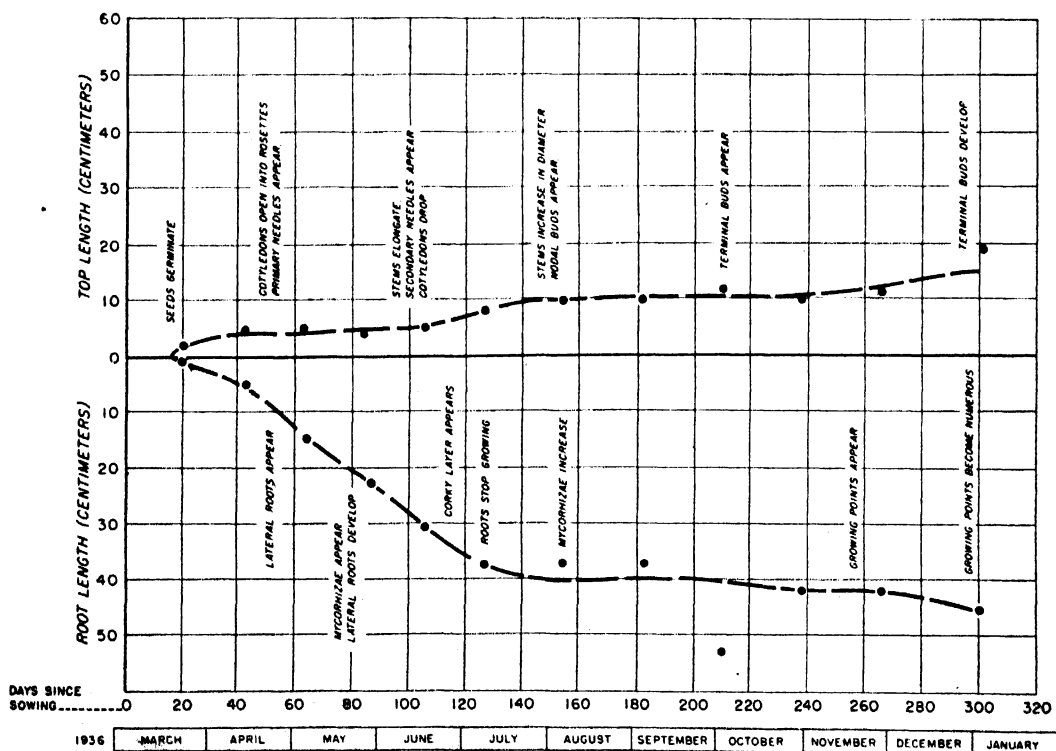


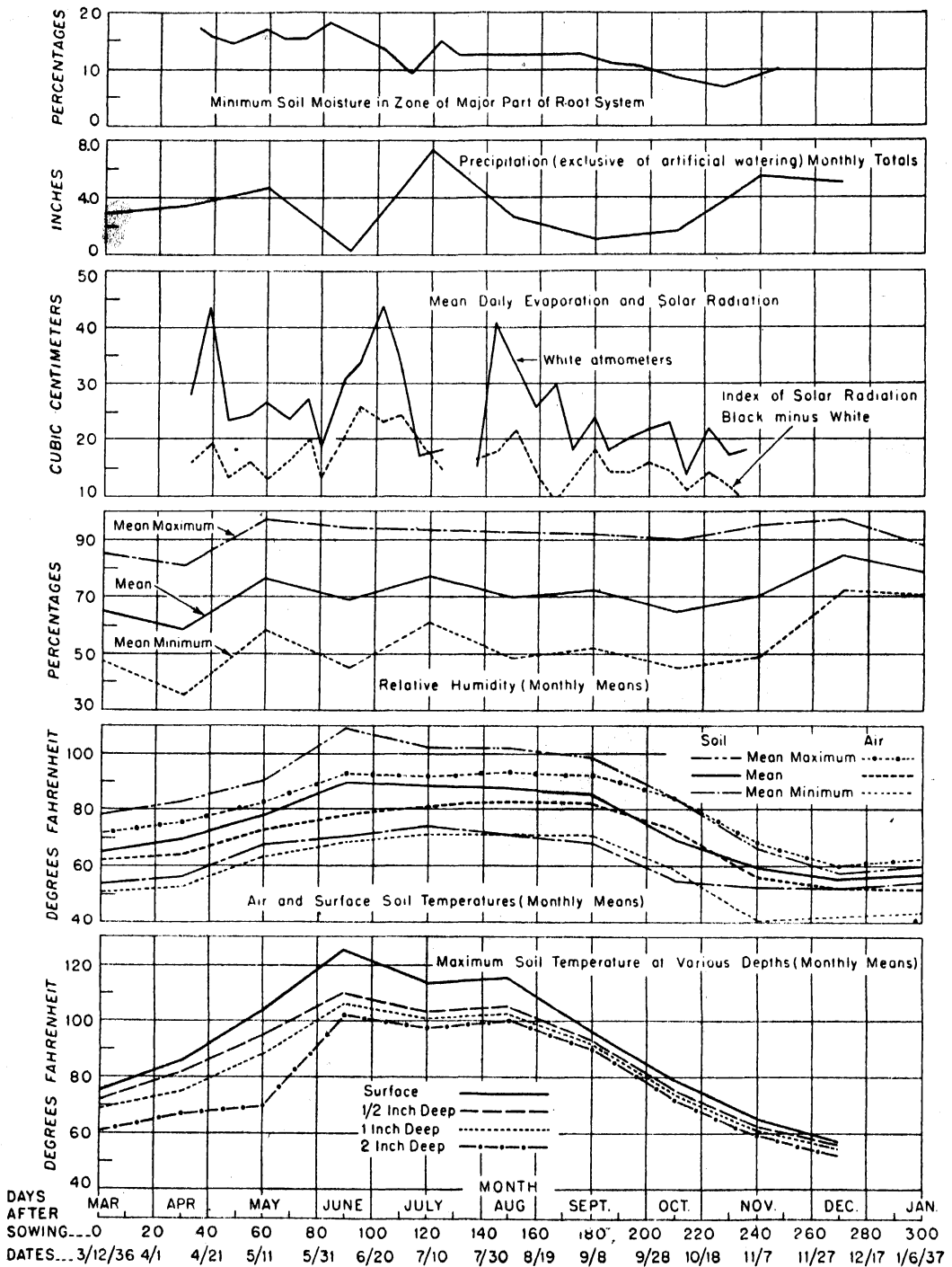FIG. 4.   Cumulative growth of tops and roots—loblolly pine.

FIG. 5.　Seedbed conditions, Stuart Forest Nursery—1936 season.

Fig. 6. Longleaf pine in cotyledon stage a few days after burlap had been lifted. Note the seed coats still clinging to the tips of the cotyledons, and in a few cases the rosette of opened cotyledons. This figure also illustrates the method by which detailed germination data were taken: exactly 100 seeds were sown in each drill (full length not shown in photograph), and each germinated seed was marked with a toothpick to permit following its fate and behavior until establishment.

(*i.e.*, in August and September), and somewhat earlier than this in loblolly and shortleaf pines. After the middle of October numerous growing points appeared on the roots. In longleaf pine the growing points appeared chiefly on the primary root; in slash, loblolly, and shortleaf chiefly on the laterals. The first frost occurred about the middle of November, but the growing points continued to develop. Terminal-bud development also continued, and in slash, loblolly, and shortleaf pines some of the terminal buds burst open to produce new shoots.

The growth curves for the 1934, 1935, and 1936 seasons show a similar pattern even though the level of the curves varies from season to season (figs. 1–4). The dates of occurrence of the various growth phases vary somewhat also (note the ar-

rows). The top growth seemed to vary less than root growth, especially in the case of longleaf pine. Root elongation was greater in 1936 in all species where comparisons could be made. Some of these variations undoubtedly are traceable to methods of sampling, but it seems reasonable to assume that differences in date of sowing, in temperature and soil-moisture, and especially the pronounced dry period in June 1936, may have had some influence.

Dry-weight determinations made of the above-ground and below-ground portions of the seedlings at various intervals during the growing season (table II) brought out an interesting point not made evident in the length measurements. The late-season increase in dry weight of both tops and roots for all species can be accounted for only partially by the increase in needle number and growing root tips. The rather obvious explanation would seem to be the storage of reserve foods during late fall and early winter. This needs to be confirmed by chemical analyses, because the time of food storage is important. The late-season root growth is in agreement with the findings of Stevens and Laing, except that here this growth continued later into the winter.

### Site Factors

Figure 5 and table III present a fairly complete picture of the seed-bed conditions. Air temperatures varied from mean averages of 47° F. in January to 83° F. in August; the mean maximum temperatures varied from 60° in December to 94° in August; and the mean minimum ranged from 41° in November to 73° in August. The highest air temperatures recorded during 1936 at the Stuart nursery were 102° in June and August, 99° in September, and 97° in July.

Surface-soil temperatures in practically every case exceeded air temperature on corresponding days. This held for mean, mean maximum, and mean minimum temperatures, except in November, December, and January, when the
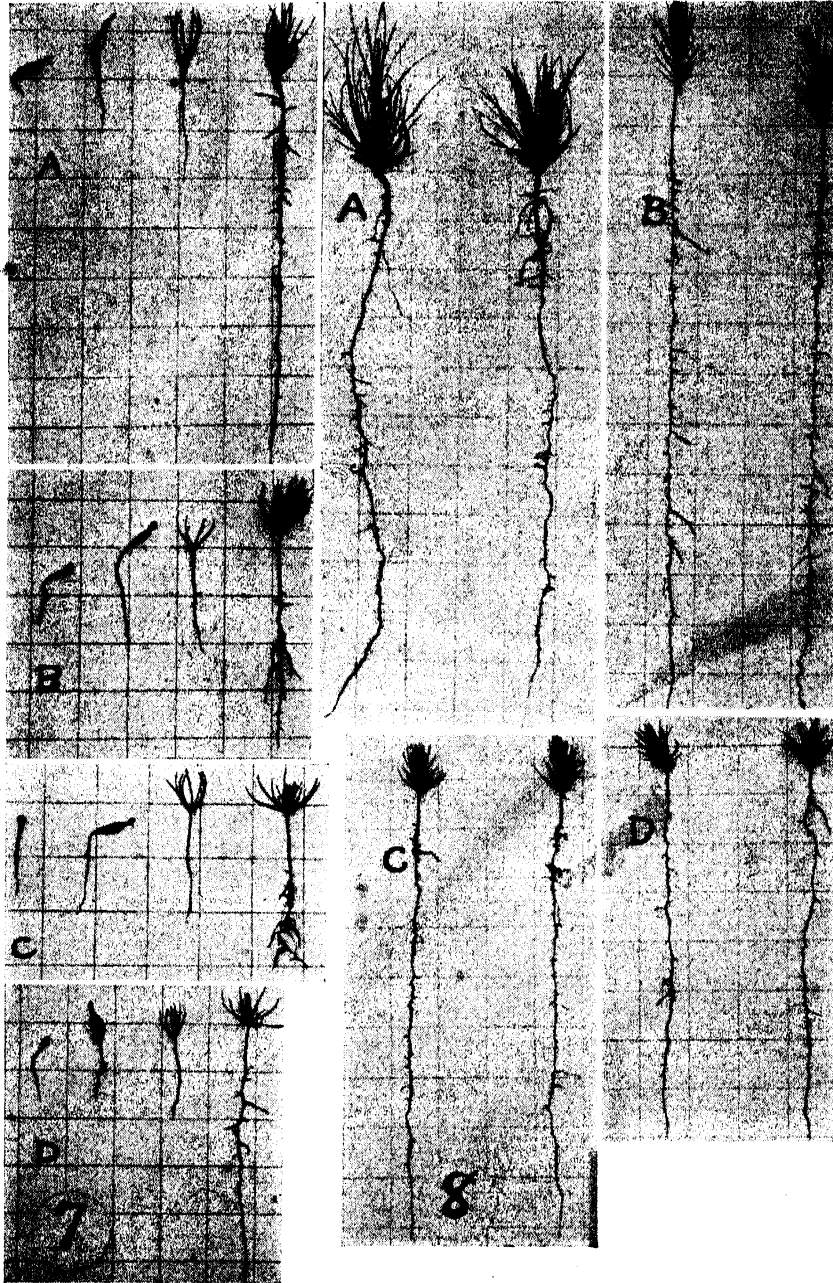
Fig. 7. Southern pine seedlings, showing four stages of development for each species: just after lifting burlap, cotyledon stage before shedding seed coat, cotyledon stage after shedding seed coat, beginning of primary needle stage. Note comparative root elongation of the four species (ruled lines 3 cm. apart). A, Longleaf Pine; B, Slash Pine; C, Loblolly Pine; D, Shortleaf Pine.

Fig. 8. Southern pine seedlings 84 days old (June 3, 1936). Period of rapid root elongation; only primary needles have developed (ruled lines 3 cm. apart). A, Longleaf Pine; B, Slash Pine; C, Loblolly Pine; D, Shortleaf Pine.

FIG. 9. Southern pine seedlings 184 days old (September 12, 1936). Secondary needle development is well pronounced; root crown and stem diameter have increased. Note also the increased root development (ruled lines 3 cm. apart). A, Longleaf Pine; B, Slash Pine; C, Loblolly Pine; D, Shortleaf Pine.

mean maximum air temperature exceeded the mean maximum surface-soil temperatures. On the daily records, it was interesting to note that in g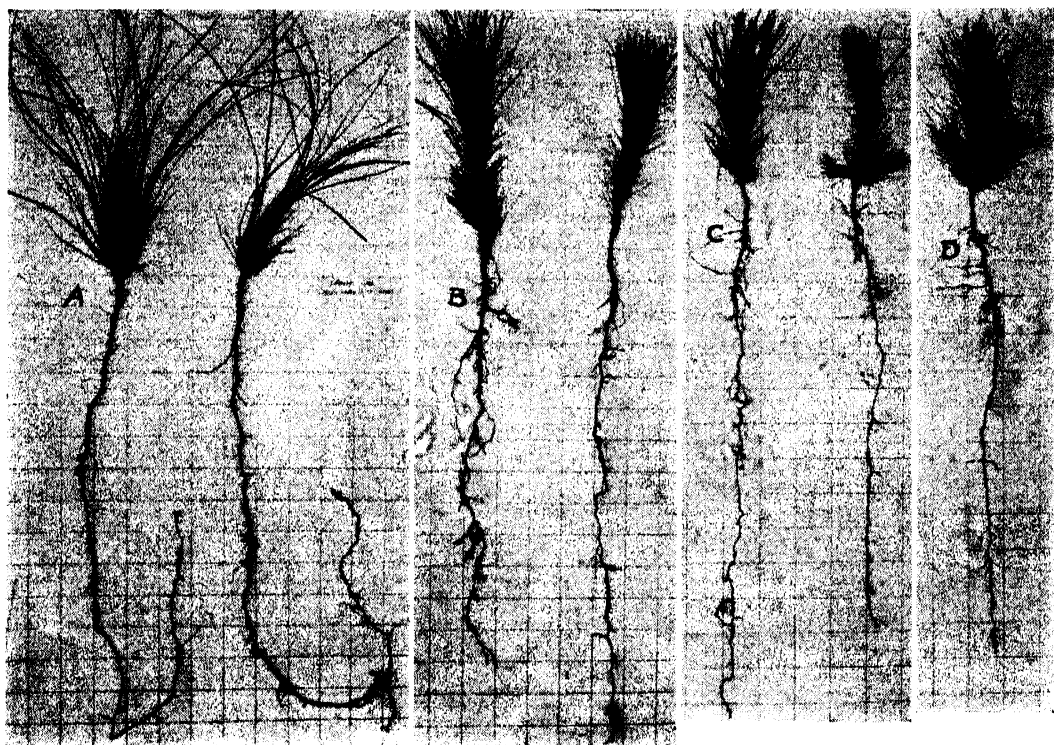eneral during the morning hours, air temperature tended to be greater than surface-soil temperatures, but in the early afternoon the reverse was true. The peak of air temperature preceded slightly the peak of surface-soil temperature. This seemed to be especially true on clear days, in agreement with the findings of Haberlandt in 1874, as cited by Lyon and Buckman ('22).

Maximum soil temperatures [3] taken at

[3] The discrepancies noted in the curves of surface-soil temperature in fig. 5 may be explained as follows: The curve in the graph of "Air and Surface-Soil Temperatures" is based on records obtained from a gas-filled thermometer placed among slash pine seedlings, while the curve in the bottom graph is based upon records obtained with a mercury thermometer

various depths show several interesting points. Surface-soil temperature was always higher than temperatures at the one-half, 1-inch, and 2-inch depths. This difference was most pronounced during the summer months of June, July, and August. As the season progressed, the differences between the temperatures at one-half, 1, and 2-inch depths became less noticeable. Although maximum surface-soil temperatures in 1935 of 120° F. or more were recorded on 39 days, and of 130° or more on 14 days, no lesions or other forms of heat injury were noted; this undoubtedly is attributable to the early development of wood and bark in southern pines.

Mean relative humidity taken with a

placed among longleaf seedlings. The differences in shading by the seedlings during the various stages of development probably account for the slight discrepancies in the two curves.

TABLE II.  *Dry weight of seedling tops and roots.  Values for above-ground and below-ground portions at indicated intervals during growing season*

| Date | Days after sowing | Top weight | | Root weight | | Top weight | | Root weight | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean (grams) | Standard deviation | Mean (grams) | Standard deviation | Mean (grams) | Standard deviation | Mean (grams) | Standard deviation |
| | | LONGLEAF PINE | | | | SLASH PINE | | | |
| **1936** | | | | | | | | | |
| Apr.  1 | 20 | .0310 | .00 | .0046 | .0032 | .0067 | .003 | .0022 | .0014 |
| Apr. 22 | 42 | .0700 | .02 | .0276 | .01 | .0256 | .00 | .0070 | .00 |
| May 13 | 63 | .1746 | .03 | .0823 | .03 | .0836 | .01 | .0458 | .01 |
| June  3 | 84 | .4115 | .08 | .1990 | .05 | .1483 | .03 | .0812 | .02 |
| June 24 | 105 | .7322 | .24 | .3168 | .09 | .2543 | .05 | .0868 | .03 |
| July 15 | 126 | 1.0315 | .45 | .3596 | .10 | .4653 | .19 | .1363 | .05 |
| Aug. 12 | 154 | 1.4112 | .43 | .5647 | .17 | .8480 | .30 | .2347 | .08 |
| Sept.  9 | 182 | 1.7570 | .73 | .7485 | .29 | 1.0577 | .38 | .3047 | .17 |
| Oct.  7 | 210 | 2.2267 | .78 | .8568 | .47 | 2.0068 | .84 | .4418 | .28 |
| Nov.  4 | 238 | 2.3558 | .81 | .9608 | .43 | 1.8595 | .92 | .5362 | .31 |
| Dec.  2 | 266 | 2.7707 | 1.08 | 1.2590 | .44 | 2.1880 | .90 | .6215 | .35 |
| **1937** | | | | | | | | | |
| Jan.  6 | 301 | 5.0258 | 2.25 | 3.3283 | 1.91 | 3.4125 | 1.96 | 1.1050 | .50 |
| | | LOBLOLLY PINE | | | | SHORTLEAF PINE | | | |
| **1936** | | | | | | | | | |
| Apr.  1 | 20 | .0038 | .003 | .0017 | .00 | .0039 | .00 | .0014 | .00 |
| Apr. 22 | 42 | .0088 | .00 | .0038 | .003 | .0089 | .00 | .0051 | .00 |
| May 13 | 63 | .0453 | .01 | .0267 | .01 | .0393 | .01 | .0262 | .00 |
| June  3 | 84 | .0940 | .02 | .0547 | .01 | .0512 | .01 | .0471 | .02 |
| June 24 | 105 | .2123 | .08 | .0998 | .02 | .1155 | .04 | .0618 | .02 |
| July 15 | 126 | .2623 | .12 | .1072 | .04 | .2170 | .11 | .0975 | .04 |
| Aug. 12 | 154 | .7150 | .39 | .2170 | .16 | .4888 | .22 | .1530 | .05 |
| Sept.  9 | 182 | 1.0565 | .49 | .2302 | .09 | .8845 | .52 | .2365 | .10 |
| Oct.  7 | 210 | 1.6988 | .79 | .4153 | .19 | 1.1438 | .50 | .3623 | .15 |
| Nov.  4 | 238 | 1.3723 | .91 | .4253 | .27 | 1.0423 | .47 | .5848 | .25 |
| Dec.  2 | 266 | 1.6797 | .71 | .7490 | .32 | 1.3595 | .56 | .8590 | .33 |
| **1937** | | | | | | | | | |
| Jan.  6 | 301 | 2.0675 | 1.23 | .8950 | .34 | 2.2392 | 1.33 | 1.6533 | 1.27 |

hygrometer exposed in a shelter 6 to 12 inches above the soil surface, was not much below 60 per cent at any time. Minimum humidity averages, however, went as low as 35 per cent. The daily course of humidity showed that the minimum ordinarily coincided with the maximum air temperature, and that the least humid part of the day was usually between 12 noon and 4 P.M. This also roughly coincided with the highest hourly evaporation rate, as recorded by atmometers.

The mean daily evaporation and relative humidity fluctuated with cloudiness and wind.  During 1936 there was a total of 99 cloudy days, of which only 31 occurred from April through September.

Precipitation (table III) is another important factor, especially from the standpoint of the amount of artificial watering needed during the growing season.  In 1936 there was a total of 42.41 inches of rainfall, distributed as shown in figure 5. Since 18.27 inches of this total occurred during January, February, November, and December, artificial watering was necessary from the time of sowing until

TABLE III.    *Weather data,[1] Stuart Forest Nursery, 1936*

| Month | Temperature (degrees F.) | | | | | | Precipitation (inches) | | | Character of days | | | Miscellaneous phenomena |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean maximum | Mean minimum | Mean | Maximum | Minimum | Greatest daily range | Total amount | Greatest in 24 hours | Number of days with 0.01 inch or more | Clear | Partly cloudy | Cloudy | |
| Jan. | 58 | 36 | 47 | 76 | 17 | 47 | 3.39 | 0.72 | 12 | 10 | 8 | 13 | Snow 0.5"; frosts, 2. |
| Feb. | 60 | 37 | 48 | 79 | 17 | 41 | 4.54 | 2.51 | 9 | 10 | 4 | 15 | Frosts, 5. |
| Mar. | 75 | 50 | 62 | 87 | 39 | 37 | 2.87 | 0.79 | 12 | 13 | 7 | 11 | Frosts, 2; thunderstorms, 2. |
| Apr. | 79 | 52 | 65 | 90 | 31 | 38 | 3.26 | 1.59 | 7 | 14 | 10 | 6 | Fogs, 2; frosts, 1; thunderstorms, 1. |
| May | 84 | 62 | 73 | 89 | 50 | 33 | 4.88 | 2.57 | 11 | 12 | 10 | 9 | Fogs, 1. |
| June | 94 | 67 | 80 | 102 | 56 | 36 | 0.26 | 0.13 | 2 | 18 | 12 | 0 | |
| July | 92 | 71 | 82 | 97 | 65 | 26 | 7.45 | 5.41 | 11 | 8 | 15 | 8 | Thunderstorms, 2. |
| Aug. | 96 | 70 | 83 | 102 | 58 | 33 | 2.63 | 1.70 | 7 | 13 | 13 | 5 | Thunderstorms, 1. |
| Sept. | 92 | 69 | 80 | 99 | 56 | 29 | 1.02 | 0.37 | 10 | 10 | 17 | 3 | Fogs, 3. |
| Oct. | 77 | 50 | 63 | 92 | 37 | 40 | 1.77 | 1.30 | 5 | 14 | 5 | 12 | Fogs, 4. |
| Nov. | 67 | 41 | 53 | 88 | 27 | 40 | 5.34 | 1.44 | 7 | 6 | 19 | 5 | Fogs, 1; frosts, 6. |
| Dec. | 61 | 41 | 51 | 73 | 23 | 38 | 5.00 | 1.53 | 9 | 12 | 7 | 12 | Fogs, 4; frosts, 6. |

[1] Data from a Cooperative Weather Bureau Station operated by the Southern Forest Experiment Station.

some time in September, when artificial watering is usually discontinued in most nurseries.

Soil moisture [4] fluctuated with precipitation and artificial watering. With one exception, the minimum soil moisture stayed above 10 per cent until late in September. This one exception was late in June, in which month only 0.26 inch of rain fell. It is concluded that during the 1936 growing season, as in other seasons, artificial watering was essential in maintaining adequate soil moisture. Crusting of the soil is undoubtedly associated with evaporation from the soil surface, and on the heavier soils it may be advantageous to cultivate or use mulch.

This picture of seed-bed growing conditions in central Louisiana may be summarized as follows: mean air temperature ranged from 47° to 83° F.; soil temperature at the surface averaged 55° to 89°; there was a high degree of solar radiation; mean relative humidity was above 60 per cent; annual precipitation was over 40 inches, more or less desirably distributed; and soil moisture, maintained with the aid of artificial watering, stayed above 10 per cent during the growing season.

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[4] The minimum soil-moisture content was determined by taking borings just prior to rains and waterings in the zone occupied by the major portion of the seedling roots.

*Discussion*

This study has focused attention upon several important points:

1. The similarity between seed-bed and laboratory germination and the comparatively high percentage of ungerminated seed both in nursery and laboratory indicate that more attention should be given to the condition of the seed prior to sowing, and emphasize the need for improving methods of extraction, handling, and *storage* of seed.

2. Watering during the *germinating* period appears to be desirable to prevent drying out of emerging radicles. Watering during the growing season needs further study in regard to the wilting coefficient, the use of moisture indicators, and the effect of various soil-moisture contents on seedling development.

3. The apparent resistance of southern pine seedlings to high surface-soil temperatures indicates that under ordinary circumstances shading is probably unnecessary.

4. Most interesting of all, are the questions which the root activity and dry-weight increase in late fall and winter raise with regard to seedling dormancy. What is seedling dormancy in southern pines, and how can it be recognized? Is it important from the standpoint of planting operations? Is there a chemical test

for it? If reserve foods are being deposited in winter, should not watering and lifting practices be reconsidered? The variability in field survival of planted seedlings would seem to warrant further study of these questions.

## SUMMARY AND CONCLUSIONS

A study of the normal growth and development of southern pine seedlings was carried on for 3 years at the Stuart Forest Nursery in central Louisiana to learn what occurs from the time the seed is sown until the trees are lifted for planting. Records of site factors, including air temperature, relative humidity, solar radiation, evaporation, precipitation, and moisture and temperature at the soil surface and at various depths, provided a fairly complete picture of the nursery-bed conditions. Curves of growth of tops and roots, with the detailed activities through the season, are presented, along with photographs of growth. These curves, along with the records of activity during germination and growth, and records of the various site factors, permit the following conclusions:

*Germination.* — Nursery-bed germination agrees fairly well with laboratory germination, so that low germination must be blamed on the condition of the seed when it comes out of storage, rather than on nursery-bed conditions. Germination takes place about 12 to 20 days after sowing and can be facilitated by watering to prevent drying-out of the emerging radicles. Lifting of burlap or other cover must not be delayed too long, and must be done with care.

*Growth.*—Root elongation takes place more rapidly than top development early in the season. There is a tendency, but with much variation, towards alternation between root activity and top activity. The increase in weight in both tops and roots late in the season is not accounted for by increasing numbers of needles and roots, but points toward deposition of reserve foods. Root growth continues after the first frost, and through the winter. Top growth varies less from season to season than does root growth, traceable in part to soil variability.

*Site factors.*—Despite high surface-soil temperatures southern pine seedlings are resistant to heat injury, indicating no need for artificial shading under ordinary circumstances. Soil moisture should be held around 10 per cent and should not be permitted to drop below the wilting point; liberal use of the watering system is indicated.

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# THE SNAIL, *NERITINA VIRGINEA,* L., IN A CHANGING SALT POND

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## Introduction

The sea throwing up sand bars may cut off ponds that may become more saline than the sea itself. Examples of such salt ponds are seen in Jamaica, B. W. I., both to the west of Kingston, where two large turbid brine ponds formerly supplied much salt for ships, and outside the harbor of Kingston, opposite "Port Royal," where is "The Great Salt Pond" close to Ft. Clarence (fig. 1). Two miles from this salt pond, at Port Henderson, the Zoological Laboratory of the Johns Hopkins University had a marine station in 1891, 1893, and 1896, which led to the discovery in the salt pond, by Dr. M. M. Metcalf ('04), of a dwarf form of *Neritina virginea* which he thought dwarfed by the great salinity, that he measured as 1.0380.

*Neritina virginea* is widely distributed as a river snail but also occurs in estuaries and even in the sea, near shore. That larger shells occur in fresh waters and smaller in salt is a conchologist's belief, not always documented by data of collecting. Measurements of the shells in the large collections of the Academy of Natural Sciences of Philadelphia show them divisible into larger specimens from 34 localities and smaller from 48 localities, in Bahamas, Bermudas, West Indies, Central America, Brazil, Mexico, and Florida; but evidence is lacking as to which specimens were taken in fresh and which in salt waters. However, the larger shells are darker and the smaller lighter in hue and the larger range from 3–25 mm., while the smaller range from 3–20 mm. Also the averages in the collections of large shells ran from 8–20 mm. and the averages in the collections of smaller shells from 4–18 mm.

Eleven of the localities were in Cuba, Florida, Bahamas and Bermudas, where



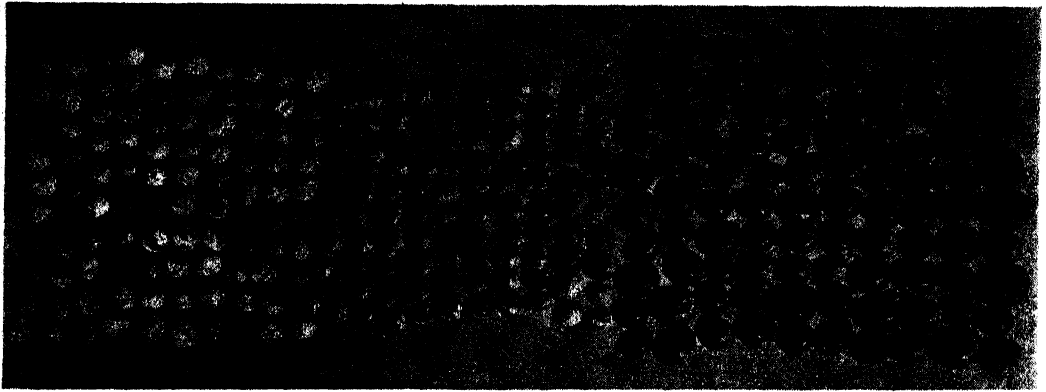Fig. 1. Photo of salt pond in 1936 (by Dr. Lynn).

FIG. 2.  Photo of groups of larger and smaller *Neritina* shells in the salt pond.

one might expect no fresh waters and the averages in these collections ranged from 4–16 mm., which seems to indicate that small size is often associated with salinity in *Neritina virginea*.

In 1910 the location of the above laboratory at Montego Bay, Jamaica, afforded opportunity to revisit the Great Salt Pond which was found no longer shut off but opening freely into the sea, though the salinity was still in general greater than in the sea.  The snails were now in two communities, the one the greatly increased descendants of those seen nineteen years before and the other not previously seen and now in less saline water and made up of much larger and darker shells.  The more extensive community, of shells smaller than formerly there, lived in very shallow water fully exposed to intense sunlight while the lesser community of larger darker shells was in somewhat deeper water slightly shaded.

At first it appeared as if in nineteen years the snails seen by Metcalf had evolved into two groups of descendants, the one still smaller, the other larger than the ancestors.

Comparing the original with the two later communities we have the three size groups seen in figure 2.  Here 100 of Metcalf's collection, to the left, occupy more space than the like number from the community of numerous very small shells, in the center, while the hundred of the

community of large dark shells takes up much the most space, as seen to the right. Moreover, as this photo shows, the Metcalf shells were much the lightest and the biggest shells the darkest.

To give numerical expression to the obvious differences in brilliance seen in these three groups, Professor A. H. Pfund measured the light they reflected as compared with that from magnesium oxide and found that the original shells, those to the left, reflected 29 per cent, the smallest, in the middle of the photo, 18 per cent, and the largest, to the right, only 9 per cent.

To gain added knowledge of the snails in this pond, after a lapse of 21 years more, with the aid of the lamented Frank Kundall, then Secretary of the Jamaica Institute, collections were made by a member of the staff of the United Fruit Company, but when they arrived in Baltimore they proved marine littoral shells, with only one *Neritina virginea* amongst 241 *Nerita versicolor* Gml., 247 *Nerita tessellata* Gml., 26 *Nerita pelleronta* L., and 6 quite young *Livona pica* L.  Had the pond been so long open to the sea as to be inhabited by littoral marine snails to the exclusion of *Neritina virginea?*  Or was there some error in collecting?

To settle such questions a third visit to the pond was made in 1932 with the aid of a small grant from the National Research Council.  The pond was found closed off from the sea, with no marine

snails and very few remaining *Neritina virginea*.

Since then the pond had been visited by Dr. W. G. Lynn, in 1936, and by Dr. d'Alte A. Welch, in 1939; and found closed in 1936 but open in 1939. Thus we have some facts as to changes in the pond through nearly fifty years and data as to changes in *Neritina virginea* in this pond. We infer that conditions in the pond modify the snail.

### DESCRIPTION OF "THE GREAT SALT POND"

In the older maps "The Great Salt Pond" is represented, in some shut off from the sea, and in others opening into it. It is a clear, shallow expanse of saline water about one mile wide, separated from the sea by a long narrow sand bank that extends, at times when the pond is closed, all the way to the rocky hill on which stands Ft. Clarence, but is separated from that hill by a channel at times when the pond is open. Back of the main pond there are one, or more, smaller, sometimes mere mud flats, that connect with the main pond by a narrow channel and are surrounded by morass. The bottom of the pond yielded to the dredge stinking mud and some pelycopods—In surface collectings were zoeas and fish eggs. The whole suggests former existence of a shallow bay cut off from the sea by the growing sand bank and some old shell marl supports this view.

The pond is still inhabited by the sharp-nosed crocodile (*Crocodilus americanus*) and by so many fish that a fisherman rents exclusive rights from the United Fruit Company and supports himself from the fauna.

The Blue Mountains shut off the moist winds from this part of Jamaica and the pond lies in a very arid region with only small growths of mangroves along its borders and on the sand bank, as seen in figure 1.

Being shallow and without shade there is rapid evaporation compensated for by rare rainfall that enters the pond without river courses. The neighboring hills also have scant rainfall and are set with small acacia and cactus growths.

The pond mouth opens and closes with irregular rhythm dependent on uncertain rainfall and upon storms and wave action, as expressed by the manager of the estate adjoining the pond, who writes—"Every time we have flood rains in St. Catherine the water forces its way into the sea and the break remains open till the water has run off. The sea then forms a fresh barrier which in due course is opened and closed in the same way."

*Description of Closed Phase of The Great Salt Pond.*—In 1891, members of the "Chesapeake Zoological Laboratory," then at Port Henderson, visited the Great Salt Pond, both by trail over the hills and by rowboat, but this had to be dragged a hundred feet over the sand bank into the pond, where Dr. G. W. Field, with night light, shot crocodiles. Inside the sand bank the water was very shallow and here schools of fish were taken with a casting net, as they seemed searching about for exit from the pond. From this shallow area there ran out into the sand bank a bay or lagoon (*C* in fig. 3) "about forty feet wide and four times as long," and lying on the bottom of this lagoon were the sedentary jelly fish described by Dr. R. F. Bigelow as *Cassiopea xamachana*.

The lagoon was bordered by mangroves on its northerly and southerly banks and in a sunny spot near its edge was the recently abandoned nest of a crocodile whose young were floating not far away. One taken with a noose and kept in captivity was more alert and active in taking living fish than the alligator of Florida. The fish and jelly fish may have been long imprisoned in this pond as time would be required to attain the density measured by Dr. Metcalf as 1.0380; and also the U. S. Hydrographic Chart of 1881 shows the pond closed as in 1891, and it may have been closed those ten years or more.

Within the pond and near the sand bank where it opens and closes and probably about the region 1 and 2 of figure 3,
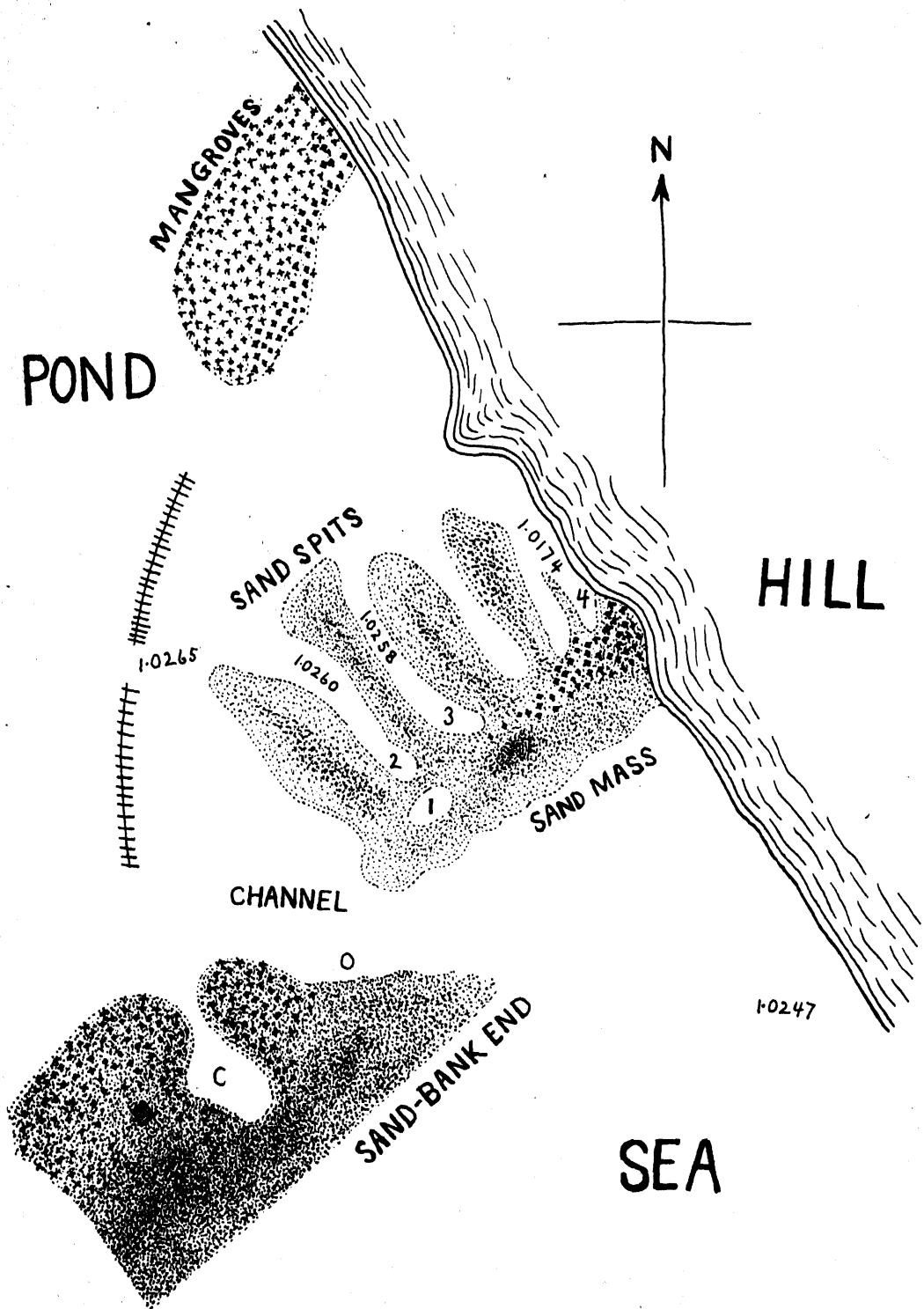
FIG. 3. Diagram of the mouth of the salt pond in 1910.

there was a small sand islet, perhaps fifty feet long. This was elongated at right angles to the sand bank and along the edge of one end of this sand islet the *Neritina* were found by Dr. Metcalf.

The closed phase was thus like the open phase seen in figure 3, except that the sand bank ran straight on to the hill and a small sand islet stood in place of the large sand mass of that subsequent open phase.

*Description of Open Phase of Mouth of Great Salt Pond.*—In 1910, the location of The Chesapeake Zoological Laboratory at Montego Bay, Jamaica, made possible a visit to the pond by a native boat from Kingston, and on September 20 the pond mouth was found open as represented in the diagram, figure 3. The sand bank no longer ran to the rocky hill but on the contrary was separated from it by a wide channel through which the tide was rising in strong currents two feet deep. Where there used to be a small islet within the pond was now the large sand mass represented in figure 3, only slightly above the water level, except in one small area of dry sand, as if wind-blown. While this sand mass ran in the main parallel to the sand bank there jutted out from it long sand spits parallel to the shore of the rocky hill and at right angles to the sand bank, leaving long shallow lagoons between the spits. Probably the old ending of the sand bank had been washed out to sea when the pond burst open and the bottom of the old shallows formed this large sand mass gullied out in lagoons by currents, blocked by the waves. Fishermen housed where the former crocodile nest had been and had built a fence across the channel to support their nets.

The main sand mass was covered with objects indicating overflow and the spits were wet and almost submerged. The lagoons were but few inches deep and all opened freely into the inner pond where the water was but a foot in depth. On the main sand mass there was a little pool (region 1) four or five feet long and

four inches deep, that smelt of sulphuretted hydrogen and at 7 A.M. had a density of 1.0273 and a temperature of 25° C., but yet was part of the distribution of *Neritina virginea* that also occurred in the lagoons at 2 and 3, figure 3.

In the channel the salinity was 1.0265 as compared with that of the closed pond in 1891 measured as 1.0380 and the sea off Ft. Clarence wharf was 1.0247. In the lagoons the salinity ran from 1.0258–1.0260 (all the densities here recorded were reduced to 15° C.). Yet, in the last lagoon, close to the rocky shore of the hill, though its water opened into the pond as did all the lagoons, the salinity at 9 A.M. with a temperature of 30° C., was only 1.0174. This exceptional condition may arise from the entrance of springs from the hill, as seen in the very copious spring of the baths at Port Henderson. A log lying in this lagoon suggested former activity of the sea.

*Subsequent Phases of the Pond Mouth.*—Twenty-two years elapsed and in 1932 we revisited the pond and found it closed much as it had been forty-one years before so that approaching the pond by auto toward the Fort one walked on from the hill over the sand bank to the fishermen's house without any interruption of channel. Yet while the sand bank had been restored as formerly, there were no islands in the pond but one waded over smooth sand bottom, in the region of sand mass lagoons and spits represented in figure 3. No snails were found in either of the two regions where they had abounded. Salinity measured just within the sand bank ran from 1.0122–1.0124 and in the sea just outside 1.0240. The mangroves from the hill shore had visibly extended out more into the pond since 1910.

The fishermen, claiming that high water in the pond was detrimental to their fishing, were at work to dig a trench to let the water out, but had a hundred feet yet to go.

Three years later, Dr. Lynn found the sand bank much the same, except that

where the fishermen had been digging, the pond ate into the sand bank as a bay that nearly met the sea, leaving so low a barrier here that the waves almost broke over it at high tide. Yet there was no inlet and boats were dragged over the sand bank to the fishemen's lagoon; however, they reported that the pond was generally open and had been recently closed by windstorm. Dr. Lynn's photos, made in 1932 and in 1936 from the hill, show that the mangroves had not only extended more from the shores but were now seen as scattered bushes out in the pond (fig. 1).

That the pond was still saline was shown by some of the *Neritina* shells bearing calcareous bryozoa and one with a living barnacle, identified February 1, 1933 by Dr. J. P. Visscher, as *Balanus amphitrite,* a salt water species adult and about six months old.

Another three years later, in 1939, Dr d'Alte A. Welch visited the salt pond and found it no longer closed but open much as in 1910, with a diagonal channel cutting off the hill from the sand bank, so that wading waist deep was necessary to reach the sand bank; and across this channel the fishermen had again built a fence for fish nets.

Thus the mouth of the pond was seen closed in 1891, 1932 and 1936, but open in 1910 and 1939. However, we have no nearer approach to actual observation of dates of opening and of closing than the fact that in 1936 the mouth was shut and three years later open again.

## CHANGES IN SNAILS

Along with the above changes in the salt pond went changes in the snail *Neritina virginea* exposed to an environment changing in salinity, in depth of water, in amount of insolation, in character of food and in adverse states of wave and sand motion.

The habitat of the snails described and illustrated in color by Dr. Metcalf is defined in his letter of 1916 as follows: "My shells were obtained from an inner

island of bare sand with very shallow water at its edges. Just at the water edge the shore of this island (perhaps fifty feet long) was literally covered with living *Neritina* so that one could hardly see the sand beneath." These snails were very brilliant and so small as to be called variety "minor." Some of them subsequently loaned me are seen to the left in the photo (fig. 2), where a random hundred are placed in a square.

To obtain some measure of the brilliance of these snails and others to be compared with them we have, as elsewhere noted (Andrews, '38), compared the light reflected by an apparently typical specimen with that reflected from magnesium oxide; this percentage is recorded as Br.

And to obtain a more complete record of the size of the shells forming a community of *Neritina virginea,* we have measured them as follows: Calipering the cross diameters of the largest and the smallest, we have the range $R$, but to express the greatest diameter over all, we measure the largest diagonally and put this down as maximum $M$. The average was got from the above range or from direct measurement of an apparent average shell, and recorded as $Av$.

Some idea of the bulk of an average shell was got by measuring the volume of as many as possible of any community, in a tall cylinder graduate, and dividing this gross volume by the number of individuals used. This approximation to the average volume is recorded under the caption $cc$. Finally, each population of these shells was rubbed through sieves of iron wire with square meshes successively of 11, 5.5, 4.5, and 3.5 mm. on a side and record was made of the numbers of shells that stuck on each sieve expressed as percentages of the whole number used, as $a, b, c,$ and $d$.

Moreover, when there were small shells, very youthful ones, that went through the smallest sieve, 3.5 mm., these were recorded as $e$. However, as all the shells found in this pond passed readily

through the mesh of 11 mm., we omit the record of this.

Now a random group of 351 from the shells got by Dr. Metcalf measured as follows:

| Br (per cent) | R (mm.) | Av. (mm.) | M cc. (mm.) | b | c | d | e |
|---|---|---|---|---|---|---|---|
| 35–40 | 3–8 | 6 | 9 | .15 | 9 | 61 | 24 | 5 |

This means that these shells reflected a very large percentage of light, as may be seen in the group to the left in figure 2, and with a range in diameters from 3 to 8 millimeters, or an average of 6 mm.; the largest had a maximum diameter of 9 mm. and they were so small that the average bulked only fifteen hundredths of one cubic centimeter and all but nine per cent went through a mesh of five and a half mm. side, while 61 per cent stuck on the mesh of four and a half mm., and twenty-four per cent went through even that and stuck only on the three and a half mesh, leaving but five per cent to pass that final gate.

The charming color and pattern adornments of these shells have been well illustrated by Metcalf ('04) and need be considered here only as far as to see if they vary in this pond through long periods. As elsewhere published (Andrews, '38), we have placed the shells of *Neritina virginea* in five arbitrary groups according to pattern, or pigment distribution.

The above 351 fall into these groups as follows:

| I | II | III | IV | V |
|---|---|---|---|---|
| 5% | 2% | 30% | 50% | 12% |

which means five per cent of these shells were all black or with but small spots of white on generally black shell, two per cent were pale with little pattern, thirty per cent had more or less evident spiral distribution of pigment, fifty per cent were adorned with angular lines on a lighter background making large areas or spots, and twelve per cent were dotted with fine areas or spots. When to the above shells we added the 31 figured by Dr. Metcalf, the entire 382 representatives of the original community show just the same percentages in the five groups.

The brilliance of these shells depends partly upon the clearness of the outer cuticle that lets the light reflect from the calcareous shell below, and upon its polish, but largely upon the amount and distribution of the pigment under the cuticle.

Recorded differences in hue may be partly due to bleaching of collected specimens but are chiefly based upon differences in amout of pigment used in the making of the shells.

Below, we describe six other collections of *Neritina* shells from this pond and observe that they are darker than the above. Yet when we took all the 36,174 shells and placed those of each collection in the above groups, we found the percentages much the same.

In all the collections from this pond the percentages in the above groups were: in I 2–13, in II 1–4, in III 5–30, in IV 45–67, and in V 8–30. Or the averages for all seven collections were : I 6, II 3, III 17, IV 57. and V 14 per cent. That is, a community is made darker not by increasing the proportion of one category, say No. I, but by adding more pigment to many shells in other groups, without upsetting their comparative frequency. Greater or less pigmentation all over the shell is determined by the mantle organs that enlarge the shell at its edge and these generally act in the same spatial mode and same intensity throughout the life of the snail.

While size changes are expressed through all the snail body, pigment changes, though they finally show all over the surface of the shell, are expressed locally only at the edge of the shell in the mantle organs that make the shell.

*The Snail Population in 1910, After Nineteen Years.*—The small island of nineteen years before was now represented by the large sand mass indicated in figure 3, with its lagoons and sandpits; and with this extension of available optimum living conditions went a great expansion of the large community of snails that now no longer was confined to the

margin of one islet but abounded on the bottom and margins of two lagoons, 2 and 3 of figure 3, and a small pool (region 1); but not in the third lagoon at all.

So abundant and crowded were the members of this community that about six quarts were taken, later measured as 5950 cc. of shells. On the lagoon margins the snails crawled out about two feet onto the wet sand and were exposed to full sunshine only moistened by the saline water. As in former times, the snails at the margins were so crowded as to obscure the sand. In the brilliant sunshine these snails were not conspicuous, since their bright shells blended with the sand and ooze. In the shallow lagoons they crawled upon the sand, the microscopic ooze, some dead leaves and slimy green, filamentous algae.

That the members of this very prosperous community were smaller than their ancestors is seen in figure 2, where one hundred at random in the middle of the photo are to be compared with the hundred of former representatives, at the left of the photo. The same number occupies less space and almost every one looks smaller than the original snails, to the left.

To show that this diminution in size applied to the whole community, we compare the random 351 specimens of the former collection with the entire community of 28,212 shells of the later collection:

| D | No. | Br | R | Av. | M | cc. | b | c | d | e |
|---|---|---|---|---|---|---|---|---|---|---|
| 1891 | 351 | 35–40 | 3–8 | 6 | 9 | .15 | 9 | 61 | 25 | 5 |
| 1910 | 28212 | 20–40 | 2.5–5.5 | 4 | 9 | .13 | 1.5 | 35 | 62 | 0.4 |

Thus, while the extreme length of some may have been equal to that of any of their ancestors, the range and average of individual diameters was less and, significantly, while 61 per cent of representatives of the ancestors had stuck on mesh of 4.5 mm., now 62 per cent of the entire community went through that mesh and stuck only on the smaller mesh of 3.5 mm., yet there were almost none extremely small and presumably very young. On some shells there were still scars of egg-capsules of the last breeding season,

up to 65 on one shell, indicating that many snails were mature.

In this pond the percentages of shells that passed through the smallest sieves were so small that we infer few immature shells were collected and hence the differences measured between different collections were not to any great extent due to immaturity of specimens.

The water that bathed these snails was still saline though not as dense as measured nineteen years before, but unfortunately we do not know how long the greater density continued before it was reduced, but if the great density brought about the original dwarfing, as assumed by Dr. Metcalf, it may have endured long enough to lead to still more diminution in size and this action may have still been in progress as the water was still more saline than that of the sea.

Yet while this main community was living in strongly saline waters there was found a smaller community in much less saline water, though in part of the same pond. That was the region (4 of figure 3) near the rocky hill where, as mentioned above, there may well have been fresh spring water emerging into the pond. Though this smaller colony was composed of larger and darker shells they were not herded in droves close to the water's edge, but scattered over the bottom and on the rocks, here and there, covered with water over a foot deep and somewhat shaded by mangrove bushes, so that the two natives who easily gathered the smaller shells out in the open could find none in this remoter region.

Snails of this colony were very much larger and darker, as noted in collecting them, and as shown in figure 3, where one hundred at random are placed at the right to compare with the smaller forms in the center quadrangle.

Again, we express the size of these large dark snails in the adopted formulation, as follows:

| D | No. | Br | R | Av. | M | cc. | b | c | d | e |
|---|---|---|---|---|---|---|---|---|---|---|
| 1910 | 6054 | 29 | 4.5–11 | 7.5 | 14 | .37 | 86 | 13 | 0 | 0 |

Though the water these snails lived in was in communication with that of the rest of the pond, it was not dense, but at nine a.m. when 30° C. gave readings of only 1.0174.

Snails were not searched for in this locality in 1891 and it seems more likely that they were represented there then, than that they had descended from the smaller shells of the more saline part of the pond. In any case there is a certain probability that such large dark snails might be introduced into this salt pond through underground passages such as are common in Jamaican limestone; in fact a few large dark *Neritina virginea* were found in 1932 in the little spring hole, with strong flow, at the very edge of the sea, at Rock Port, east of Kingston; and it is said that this spring had a recent origin in connection with the great earthquake of 1907.

*Subsequent Status of* Neritina *in the Great Salt Pond.*—In June 1932, *Neritina virginea* had nearly vanished from the salt pond, for wading over the sand flats that now occupied the original site of the big community, no snails were to be found and the same was true in the region 4, near the rocky shore. But eventually 382 *Neritina* were found in the lagoon near the fishermen's house (*C* in fig. 3). These were not aggregated at the water's edge but scattered five or six to a square decimeter over the bottom.

Comparing these with the former great community, they are sufficiently near the same in size to have been part of an original community transported to their present abode on boats or other floating objects.

| D | No. | Br | R | Av. | M | cc. | b | c | d | e |
|---|-----|-----|-------|-----|---|-----|-----|----|----|---|
| 1910 | 28212 | 20–40 | 2.5–5.5 | 4 | 9 | .13 | 1.5 | 35 | 62 | 4 |
| 1932 | 382 | 29 | 3.5–7 | 5.5 | 9 | .10 | 2 | 45 | 51 | 2 |

Four years later, June 25, 1936, Dr. Lynn again found snails in the region 4, near the rocky shore, where there was now a muddy bottom and some abandoned shells of *Melampus*. But the only three found in the region where they had swarmed before were dead shells occupied

by hermit crabs and these shells were of the size and darkness of those at the region 4, so were doubtless transported by the hermits from that locality of dark larger shells.

However, at a region near that marked 0 in the diagram 3, where fishermen drew up nets on a little beach, *Neritina* were found which may be reckoned as survivors of the large community of the lagoons at 1, 2, 3. Also, the snail community at the lagoon C, was still in existence. There are thus three communities to be compared with the former, or ancestral ones.

First, the shells near the hill shore, 4, are to be compared with those there in 1910, as none were found in 1932, as follows:

| D | No. | Br | R | Av. | M | cc. | b | c | d | e |
|---|-----|-----|-------|-----|---|-----|-----|----|----|---|
| 1910 | 6054 | 29 | 4.5–11 | 7.5 | 14 | .37 | 86 | 13 | 0 | 0 |
| 1936 | 124 | 21 | 3 –10 | 6.5 | 13 | .21 | 62 | 17 | 13 | 7 |

Thus after 26 years the shells in this place were much smaller, and also darker; to the eye they look much darker and two to four times as large as those at 0. Then the colony at 0 is compared with those in the large community formerly not far from this place, as follows:

| D | No. | Br | R | Av. | M | cc. | b | c | d | e |
|---|-----|-----|-------|-----|---|-----|-----|----|----|---|
| 1910 | 28212 | 20–40 | 2.5–5.5 | 4 | 9 | .13 | 1.5 | 35 | 62 | .4 |
| 1936 | 222 | 20 | 3.7 | 5 | 9 | .09 | 2 | 16 | 68 | 12 |

The measurements are conflicting; to the eye they look much alike, but a larger number entered the smaller sieves and the average may have been less than formerly. Finally, though shells of 1936 look smaller and lighter than in 1932, the conflicting measurements of the snails at the remoter locality C, show little change in four years.

| D | No. | Br | R | Av. | M | cc. | b | c | d | e |
|---|-----|-----|-------|-----|----|-----|-----|----|----|---|
| 1932 | 382 | 29 | 3.5–7 | 5.5 | 9 | .10 | 2 | 45 | 51 | 2 |
| 1936 | 795 | 29 | 3.5–10 | 6 | 12 | .10 | 6 | 22 | 61 | 9 |

There is no reason to suppose that the diminution in size of the members of these populations was brought about by any enemy selecting the larger individuals. The largest community seemed to have ideal condition for increase to an extreme density of population and their destruc-

tion was due to human interference along with subsequent storms causing bottom changes. In the colony in less saline water, there were about six per cent of dead, or abandoned shells, in 1910, and ten per cent showed signs of healing of broken shells; and of the 124 taken in 1936 this percentage rose to 11. Such broken shells might have been caused by storms but there may be enemies such as possibly the white crab (*Cardisoma guanhumi* Lat.) which was seen there. The small round depressions seen on some small shells opposite the orifice were experimentally reproduced by strong pressure of one of the great claws of that crab.

The pigment found in these shells is in some few individuals red, pink, or purplish and, apparently, when the amount of pigment is lessened in the smaller shells there may be also a substitution of red for black; at least, when 906 random shells of the larger dark colony at region 4 were compared with the same number of the little shells from regions 1, 2, 3, the red ones in the former were but 2.8 per cent and in the latter 4.4 per cent. Thus the little shells had lost not only amount of pigment but had employed more red in place of black.

## SUMMARY AND CONCLUSIONS

A small variety of the snail *Neritina virginea* L. living at the mouth of a salt pond, that tends toward a mangrove swamp climax, but opens and closes at long irregular intervals, is subject to saline environment that at times is optimum for formation of large communities but at other periods very adverse.

After nineteen years a very large community of these snails was represented by individuals smaller than their predecessors; here *deterioration in size took place* in saline environment under conditions optimum for increase in individuals. At this period beside the large community in strong saline water, there was another in less saline water: the former was composed of smaller and the latter of much

larger snails: *greater salinity being accompanied by smaller size.*

The snails first observed had shells of very light hue, but those that followed them after nineteen to forty-five years had somewhat darker shells and *the shells in least saline water were very much darker.* The snails originally found lived in greater density than any of the others, thus *greatest brilliance was in water of greatest density and least brilliance in water of least density.*

In all communities in this pond the relative percentages of individuals with black shells and with shells of various other distributions of pigment varies but little and thus the darkening of average shells in any community is due, not to great increase of "the black sheep," but to employment of more pigment in the construction of other pattern groups of that community.

In this pond both size and pigmentation change, after long dwelling in saline environment, but the maximum diminution in pigmentation did not occur with the greatest diminution in size but years before; that is, after the maximum diminution in pigment the shells continued to become smaller but again added pigment.

In this pond the saline environment is a complex of factors including not only salts in solution but differences in bottom and depth and clearness of water influencing food. Variations in depth carry concomitant differences in sunlight received by the snails, a few inches of water absorbing especially the actinic rays to a marked degree.

The largest *Neritina* snails in this pond are small in comparison with those found in larger rivers in Jamaica and if we assume that such large river snails gave rise to these dwarfs we might picture some such evolution as follows:

Large *Neritina* with dark shells gaining entrance to this pond in some remote period, possibly through subterranean channels, dwindled in size in somewhat brackish places, but long remained dark in such transition stage as recently found

near the rocky shore. Later some migrating into the shifting shallows of the mouth of the pond, dwindled more and more in size, and became deprived of much pigment down to the maximum observed in 1891. Subsequently, when the water ceased to be extremely saline, many of them again acquired somewhat more pigment but continued to lose size.

While this natural experiment shows saline environment leads to diminution in both size and amount of pigmentation it does not show what parts of the saline environment are most potent. It may be that insolation plays a leading role in the reduction of pigment!

The varying depth and clearness of water in which *Neritina* lives must be accompanied by differences in insolation and this might explain the maximum blanching of shells that was attained before the maximum diminution in size, which might have been due to other factors in the saline environment. However, since proof that increased insolation leads to diminution in pigmentation is not yet forthcoming, both change in hue and in size must still be referred to "saline environment."

That changes in salinity may be followed by changes in animals was seen in the famous brine shrimp, *Artemia* and later *Vernon* concedes that decreased salinity does produce structural changes in this animal. He also found that echinoderm plutei grew bigger in dilute sea water and probably slightly smaller in concentrated sea water.

In the mollusca, Flattely and Walton state that mussels in the Dovey river attain marketable size only when far up the river; bivalve shells in unfavorable salinity being stunted and deformed. And Bateson inferred that the shells of *Cardium edule* in dense salt water had thinner shells, with increased coloration, and modified shape. Newcombe found the shell weight of *Mya arenaria* L. in the Bay of Fundy near twice that in the Chesapeake Bay, yet the body weight is greater in the Chesapeake Bay than in the

Bay of Fundy. While the salinity in the Bay of Fundy is about 32 per mille as compared with 11 in the Chesapeake, Newcombe advances reasons for concluding that other factors than salinity must produce the differences in weights.

Finally, in the Gastropods, we learn Vernon states that Gibbons found the shells of some tropical Littorina to be thinner, brighter, and with more varied colors in brackish than in sea water; and later Federighi found the shells of *Urosalpinx cinerea* smaller in the more saline waters of Beaufort, N. C. than in less saline waters of Norfolk, Va. He argues that the opposite results obtained by Hubbs and by Huntsman for fishes in which the size is greater in more saline waters may be connected with the wide migration of fish. It should be noted also that Federighi adds that *Urosalpinx* recently introduced into the oyster beds of Blackwater river, England, in waters denser than at Beaufort grow to a larger size than even at Norfolk.

He also does not claim that the size differences in *Urosalpinx* are due solely, or even partly, to salinity, since other factors may be the controlling factors. And as such he mentions sunlight, which indirectly determines the amount of vitamins available in different algae: or there may be decisive differences in the chemical constituents of the two waters.

Federighi would extend the term sternomorphs, suggested for cramped forms by Bartsch, to include these dwarfed forms in saline waters.

Many more examples of responses by molluscs to changes in salinity are cited by Pelseneer (11). From this evidence it appears that some molluscs respond differently from others, but that in many there are changes in size following changes in salinity.

Whether all the changes in *Neritina virginea* that follow life in saline environment are due to the salt factor or not, should be determined by experiments as soon as the feeding and breeding of these snails can be controlled in the laboratory.

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# A RAPID METHOD FOR EXCAVATING ROOT SYSTEMS OF NATIVE PLANTS

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The obvious difficulty involved in observing the gross morphology of the roots of plants has made it impossible for that study to keep abreast of the remainder of the field of ecology. Many problems of competition, responses to soil structure and water conditions, effects of mineral concentrations, etc., can be solved only by intensive and widespread observation of root systems. These problems remain unsolved due to the lack of adequate methods for root excavation and collection of sufficient data.

By far the greater part of the successful observations of root systems have been made in the prairie states and provinces of the United States and Canada. In these areas the relatively uniform conditions favor the acceptance of a few data as representative of a wide area. To understand the whole of root ecology it will be necessary to carry the work of excavation into all the geographic areas of the continent and to make dozens of analyses where one has been allowed to suffice in the past. In those physically diverse areas in which soil texture, mineral localization, water content, etc., differ markedly within short distances, it is essential that large numbers of observations be made to insure the inclusion of all variables.

That such an extensive undertaking be attempted by Weaver's "trench-tracing method" ('15, '22) or by Pavlychenko's "soil-block washing method" ('37) is neither practical nor necessary. In soils with an appreciable clay content Weaver's method is utterly impractical. Both these methods require long periods of tedious work and entail great expense in equipment or labor or both. Pavlychenko ('37) has reviewed the development of root excavation methods. His account may be summarized by observing that no

method has yet been presented which does not involve one or both of the following two objectionable features: (1) excessive labor, time, and expensive apparatus; (2) unsuitability of the procedure to the study of root systems of wild plants in undisturbed habitats. With both these objections in mind the authors devised a rapid and inexpensive method which may be used under natural field conditions. The apparatus was employed in a reconnaissance survey of grass root systems in south Texas in 1930. The twenty-odd excavations under varying soil conditions proved conclusively the suitability of the method. Since then, Stoechler and Kluender ('38) developed a procedure similar to the one here described. Their apparatus has the distinct disadvantage of requiring a large quantity of water and of being too crude for use in the excavation of fine roots. Further, it involves the complete removal of the root system without affording at any stage an opportunity to take a quantitatively accurate measurement of a sample of the system *in situ*. The complete collapse of excavated root systems makes it highly desirable to make all critical determinations before the roots are deprived of the support of the soil.

## METHOD

The method may be called the "bisect-wash method." A smooth face of soil is cut through the plant axis vertically to sufficient breadth and depth to insure inclusion of the farthest ramifications of the root system in the plane of the bisection. Horizontal and perpendicular lines are marked off on this face with cord, the interval suited to the size of the root system. Then by means of a fine jet of water the soil is removed from

the whole of the face of the bisection to a depth of one or two inches. The result is a bisection of the root system which may be drawn in detail. A second face perpendicular to the first gives a half bisection which may be used as a check against the first to insure a representative sample of the entire root system.

### APPARATUS

An essential feature of a satisfactory, inexpensive method of root excavation over wide areas is the use of apparatus which can be easily transported to remote localities. Therefore the apparatus about to be described (figs. 1 and 2) was designed to fit in a small automobile with enough space to spare to allow the transportation of ample camping equipment for one or two persons.

The apparatus necessary to produce the fine jet of water consists of a forty-gallon tank (a hot-water storage tank may be used) to which have been added: (1) an air-tight bung for filling, (2) an automobile tire valve-stem for applying air pressure, (3) a gauge capable of registering 50 pounds pressure, (4) an outlet with valve to which is attached a forty-

foot length of rubber pressure hose. To the distal end of the hose is attached a nozzle consisting of a valve, a 1 × 5 inch brass barrel (handle), and a five-sixteenths inch brass tube into the curved end of which is screwed an acetylene torch tip (several sizes of apertures may be secured for different soil conditions).

Pressure may be applied to the tank by a small compressor attached to the motor of the automobile. A belt-driven compressor on the running board powered by a pulley from the hub of the rear wheel proved unsatisfactory because of the inability of the compressor's bearings to withstand the pull of the belt. A system of gears from the fan drive is much more satisfactory. Dealers in second-hand machinery can furnish small compressors originally designed for attachment to automobile motors.

A filling-station air compressor unit including a gasoline motor-driven compressor and the reservoir compactly mounted on a sufficiently heavy base constitutes an ideal portable system which may be easily fitted to a trailer or carried in the back of a pick-up truck. This apparatus permits pressures up to 100 lbs.
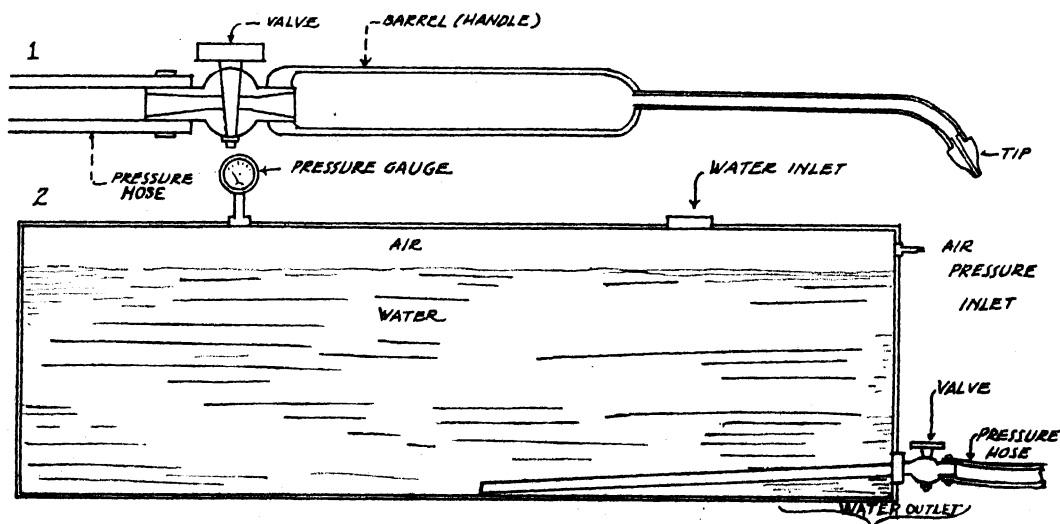


FIG. 1. Nozzle attached to a rubber pressure hose and fitted with a valve and an acetylene torch tip.

FIG. 2. Water tank fitted with a pressure gauge, a water inlet, an air pressure inlet (automobile tire valve-stem), and a water outlet.

or more without any danger, and may readily be adapted. It is far superior to the makeshift apparatus which we devised because of the shortage of funds. It might be added that its cost is very modest.

## OPERATION

The apparatus having been assembled, excavations may be made at the rate of one in one to three days, depending upon the amount of digging required. Freshly made road cuts offer excellent sites for excavation providing permission is first secured from the highway officials. Washed-out creek banks and deep erosion channels are similarly well adapted, but in all cases care must be exercised to choose plants sufficiently distant from the bank to eliminate any danger of desiccation or other unnatural effects. Trenches dug in unbroken areas are preferable but require more time and labor.

A smooth vertical face is cut through the base of the plant as described above. Before attempting any washing, especially in the case of tight clay soils, it is desirable to splash several quarts of water over the soil face at intervals of five or ten minutes until the surface inch of soil is somewhat moistened. The cords used in marking off the coördinates on the soil face are then put in place and anchored with large nails. The washing process may then be begun. It is desirable to begin washing at the top in order to minimize the danger of slumping and to allow the waste water to soak the subsoil and thus facilitate its washing. Fibrous root systems, such as those of grasses, are readily revealed by the removal of an inch or two of soil from the face of the bisection. Taproot systems might not be adequately represented by so shallow an excavation. In some cases it is desirable to cut the soil face in a tangential plane several inches *in front* of the center of the root system and to excavate by washing to a tangential plane several inches beyond the diametric plane of the root

system. Small root systems may be taken out in their entirety.

The jet of water should be sufficiently fine to avoid damage to even the finest roots. Different sizes of tips should be tried in order to ascertain the most suitable. The strength of the jet may be further controlled by partially closing the valve at the base of the nozzle. One tank of water (not over 35 gallons in the forty-gallon tank), repeatedly pumped to 40 pounds pressure as the water is used, will suffice to excavate the average grass or herbaceous dicot root system.

The revealed bisection of the root system may be drawn to scale on a large sheet of paper with coördinates corresponding with those on the bisection. This facilitates accuracy in freehand drawing. Rough pencil drawings may be labeled throughout with notations as to number of branches per inch, thickness of roots, etc., but the more important features of the root system are readily discernible in carefully made and subsequently inked drawings. Photographing, with so little contrast as is offered by fine roots against a background of soil, is unlikely to prove satisfactory.

The ease with which large root systems may be excavated by the "bisect-wash method" (grass root systems five feet deep having been excavated from tight clay in six hours) makes this method highly superior in certain types of investigations to those previously employed. Where the plant to be studied occurs on level ground, there is no reason to believe that a bisection is not an accurate and true sample of the entire cylinder of which the bisection is a diametric plane. If any doubt exists, the excavation of an additional radial plane at right angles to the first should prove the representativeness of the bisection regardless of the situation. The method may be employed in conjunction with soil analysis by securing ample soil samples from the site in the process of cutting the bisection preparatory to the washing procedure.

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# THE FEEDING HABITS OF LARVAL NEWTS WITH REFERENCE TO AVAILABILITY AND PREDILECTION OF FOOD ITEMS

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The food of most species of animals appears to depend upon quantity rather than quality. Quite a number of food habit investigators have empirically stated that animals exercise a pronounced predilection for certain foods, merely because these items constitute the greater bulk of the stomach contents. On the other hand, there are many that hold with McAtee ('32) who writes:

Within size limits, animals of practically every kind accessible to birds are preyed upon, and as we consider the records for group after group a tendency for the number of captures to be in proportion to the abundance of the animals concerned is unmistakable. Availability undoubtedly is the chief factor involved in the choice of foods, and predation tends to be in proportion to population.

Few experiments have been designed to test out either thesis, and when such have been attempted, the results have been largely invalidated due in large measure to the unnatural conditions under which the experimental animals and their prey were confined.

Extreme difficulty is encountered when one attempts to correlate available food and that eaten by terrestrial species, such as birds, mammals and certain anurans. The investigator has so many prey items to collect, and these are often so well hidden in obscure situations that research on availability and predilection, using terrestrial vertebrates as test animals, can hardly be considered trustworthy. Macroscopic aquatic life is less abundant, certainly in number of species. The lesser animal and plant life is often concentrated with predators, yet is sufficiently varied, both in number of species and in actual numbers of prey to permit any predilection on the predator's part.

This paper attempts to analyze the problem of the relationship between predation and availability through studies in the normal environment of the test subjects. Larval newts (*Triturus viridescens*) were selected as the experimental predator, and all animals and plants of a size sufficient to be ingested by the newts were accepted as the prey.

## METHODS

The present study was made in a shallow permanent pond at Ringwood, seven miles east of Ithaca, New York. This pond, covering about an acre, supports a varied flora and fauna and has long been a favored station for Cornell University biologists. During the summer it is covered with a mat of *Lemna* and the smaller *Wolffia*. Beneath this shelter lives a varied fauna of small macroscopic invertebrates, some swarming at certain seasons and absent at others. To this pond the newts repair in great numbers during the early spring, laying their eggs singly in the axils of *Elodea* and other submergent aquatics. By late July the larval newts have attained a length of 25 to 45 mm.

In collecting the newts in mid-July of 1939, a large galvanized iron scoop, with $\frac{1}{16}$ inch mesh, was used. The newts were taken during mid-morning, mid-afternoon and again early in the evening. All were secured in depths of from 4 to 8 inches of water, in the same situations where food samples were later secured. Nearly 500 were secured, 300 of which were examined for food. Those which were studied averaged 35 mm., the extremes being 32 and 37 mm., respectively. By selecting animals of nearly comparable size, there was considerably less liklihood that any discrepancy in the size limits of the prey would occur.

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To secure the available food samples, a vegetable strainer with $\frac{1}{20}$ inch mesh was used. Three hundred samples were made, half of these being taken from the bottom and half midway between the bottom and the surface. Before taking the samples, the film of *Lemna* and *Wolffia* was largely removed by hand. Small forms such as *Cyclops* and *Cypris* had little opportunity of passing through the mesh, as detritus usually effectually occluded the screen and prevented passage of any macroscopic species. These samples were placed in a large milk can and shortly fixed in a five per cent solution of formaldehyde. The contents of the can, after vigorous agitation, were placed in quart jars. Samples from these were in turn examined in large petri dishes under the binocular. Three hundred samples were examined, and all specimens which were capable of ingestion by the larval newts, as determined by earlier stomach analyses, were set aside for enumeration. In this maner it is believed that a fair sample of the available food was obtained.

The several obvious though minor objections to this method could not be easily overcome, and it is believed the results obtained are trustworthy and significant.

The stomachs of the larval newts were removed and examined under a low powered binocular microscope. The rate of digestion in the stomach is seldom sufficient to make analysis impossible, and, inasmuch as these animals bolt their food entire, little difficulty was experienced in identifying the contents. Variation in the rate of digestion is apparent, the molluscs being far more resistant to the digestive juices than such forms as the soft bodied midge larvae. Hess and Rainwater ('39) have pointed out the desirability of recognizing this differential rate of digestion when studying food predilections of fish. For this reason, an analysis by bulk might produce misleading results. The hard chitinous head capsule of the midges are resistant, and persist

after the rest of the animal has disappeared. Thus the actual count of the various animals in the stomach will give the best criteria of availability, provided there is no predilection by the newts. The important fact to be born in mind by investigators of food habits is that the feeding behavior of many species depends not only upon the quality but upon the quantity of their prey. Elton ('35) remarks that the lower limit to the size of an animal's food is partly determined by the ease with which the latter can be caught, and this in turn is tremendously affected by its abundance, for if the prey is too scarce it takes too long to collect enough to satisfy the animal's needs. It might be added that if such small prey is not readily accessible it will likewise be passed up for food which is more easily secured.

In determining the food items available to the larval newts, some index as to the size of the prey which these newts could consume had to be recognized. Accordingly the largest specimen of each species which was taken from the stomachs was considered the maximum size the newts could conveniently manage. On the basis of such reckoning, the populations of available prey were determined, and their actual numbers arrived at through 300 random samples.

Through counts of each food item from the 300 samples, the following figures were obtained: *Wolffia*, 10710; Ostracods, principally *Cypris*, 9228; Midge larvae and related forms, including Chironominae, Orthocladiinae and Tanypodinae, 5135; *Diaptomus*, 5316; *Nostoc*, 3639; Snails, including Planorbidae and Lymnaeidae, 2307; *Pisidium*, 911; *Cyclops*, 728; *Culex*, 426; *Plea*, 289; Beetle larvae, including *Tropisternus, Haliplus* and *Hydroporous*, 241; *Daphnia*, 232; and Hydrachnids, 94. Although there were many more of most of these forms in the samples that are listed above, only those which were believed capable of ingestion by the larval newts were counted.

## ACCESSIBILITY OF FOOD

It is easy to visualize that some of the possible food items might not be taken by the newts because of inaccessibility. The newts appear to take only active or semi-active forms and those which are hidden in the detritus of the pond bottom, or lie quietly in the aquatic vegetation might readily escape predation. Accordingly, a ten gallon aquarium was prepared as near as possible to a condition approximating pond conditions, into which were introduced numerous samples of small aquatic life. When the different species had become well established in their normal sphere, twenty larval newts were introduced which had been captured in the pond from which the samples had been secured. Several lengthy periods of observations provided a clue to their actual feeding habits, a procedure which would have been quite impossible under natural

conditions. It was soon patent that these larval newts took the forms most active and appeared, at least to the writer, to exercise little interest in those which lived a quiet life. The newts would often settle to the bottom of the aquarium, resting for a moment on a partly decayed leaf. This slight disturbance would set in motion an ostracod which was promptly pursued and eaten. Active mosquito larvae would attract the newts only when they were in apparent vision. The sphaerid *Pisidium,* lying quietly on the bottom, attracted the newts far less than the more active planorbid molluscs, which seem in constant, albeit slow, motion. Midge larvae and related forms were eaten with great avidity, but only when they appeared to exercise sufficiently to attract the attention of the newts.

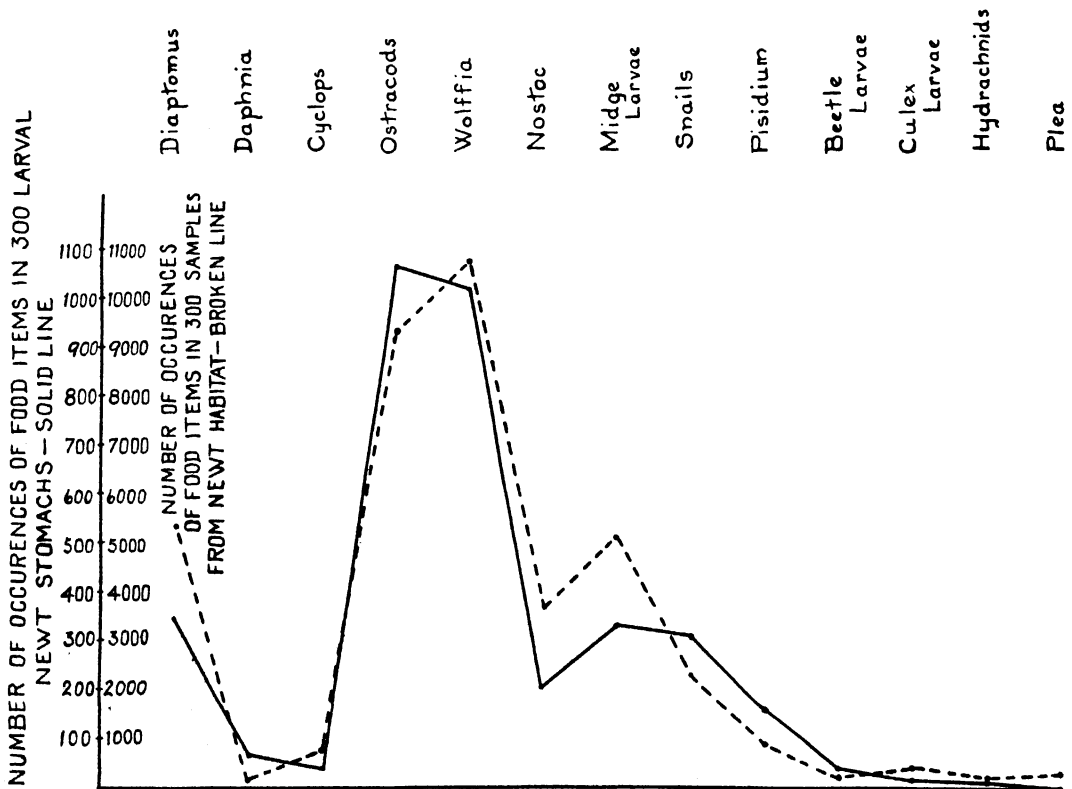In brief, the most active forms were taken more promptly than those less ac-



FIG. 1. Relation between prey species eaten by larval newts and prey populations. The close correlation between the two indicate that availability largely determines what species are eaten.

tive, but this was not wholly true of all the animals preyed upon. The incessant activity of hydrachnid mites caused them to be pursued and consumed whenever they came near the newts, and the fact that they were relatively scarce at the time the samples were made is probably the only reason why these small forms were taken so seldom. Leeches were relatively inactive, and though numerous individuals were taken in the samples, and a fair number of small size were placed in the aquaria, none were seen to be eaten.

Accessibility, through activity, probably determines in large measure what the newts eat, but that this is not necessarily altogether true is shown by figure 1, *which indicates availability generally determines those species which will be eaten.*

A list of those foods eaten by the newts examined, together with the average relative size of each item is found in table I.

TABLE I. *Relative size of different food items eaten by larval newts*

| Ostracods | Cyclops | Diaptomus | Daphnia | Hydrachnids | Wolffia | Culex | Nostoc | Midge Larvae | Plea | Beetle Larvae | Pisidium | Snails |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1.5 | 2 | 5 | 6 | 6 | 6 | 8 | 8 | 12 | 12 | 14 |

Size will naturally determine, in part, what a predator will feed upon. If the prey is too small, too great an effort must be exerted to secure sufficient numbers in a given time to appease the appetite of the predator. If the prey is small yet sufficiently numerous the predator will find it profitable to feed on such.

In determining the size ratio of one prey item to another, the average size of 50 individuals of each species was considered. The size estimate of each species thus seems reasonably accurate. Assuming ostracods and copepods to have a size of one, *Nostoc* and *Culex* larvae have a size of six; thus the latter average six times larger than the small entomostraca. Knowing the actual numbers of each group examined, both from pond samples

and stomach analyses, it is possible to plot the bulk of the pond samples against the bulk of the stomach samples (fig. 2).

## FOOD HABITS OF LARVAL NEWTS

The feeding habits of adult newts have been studied by several investigators (Reese, '12; Pope, '24; Morgan and Grierson, '32 and Hamilton, '32) but apparently nothing has been written on the food habits of larval newts, a fact which is essentially true of most larval salamanders. The stomach contents of the small newts which form the basis for this paper contained a fairly wide range of lesser aquatic creatures, these being taken in the order of their availability. Size only appears to limit the creatures upon which these larval amphibians subsist.

TABLE II. *Stomach contents of 300 larval newts taken at Ithaca, New York, from July 17–July 26, 1939*

| | Number of individual occurrences in stomachs | Per cent by bulk | Per cent frequency occurrence in stomachs |
|---|---|---|---|
| Ostracods | 1068 | 9.84 | 69.3 |
| Wolffia | 1020 | 15.80 | 65.7 |
| Diaptomus | 346 | 6.80 | 57.6 |
| Chironomidae larvae and allies | 329 | 22.30 | 54.0 |
| Snails (small Planorbidae and Lymnaeidae) | 311 | 21.06 | 45.4 |
| Nostoc | 204 | 2.60 | 8.6 |
| Pisidium | 162 | 15.94 | 20.7 |
| Daphnia | 61 | .70 | 20.7 |
| Beetle larvae (Dytiscus, Haliplus, Tropisternus, Hydroporus) | 42 | 1.60 | 4.3 |
| Cyclops | 39 | .25 | 8.0 |
| Culex | 16 | 1.30 | 3.7 |
| Hydrachnids | 13 | .60 | 3.3 |
| Plea striola | 3 | .70 | 1.0 |

In table II are listed the food items found in the stomachs with indication of their actual numerical occurrence, percentage by bulk and the per cent frequency of occurrence in the entire lot examined.

It is apparent from this study that larval newts feed upon the most available
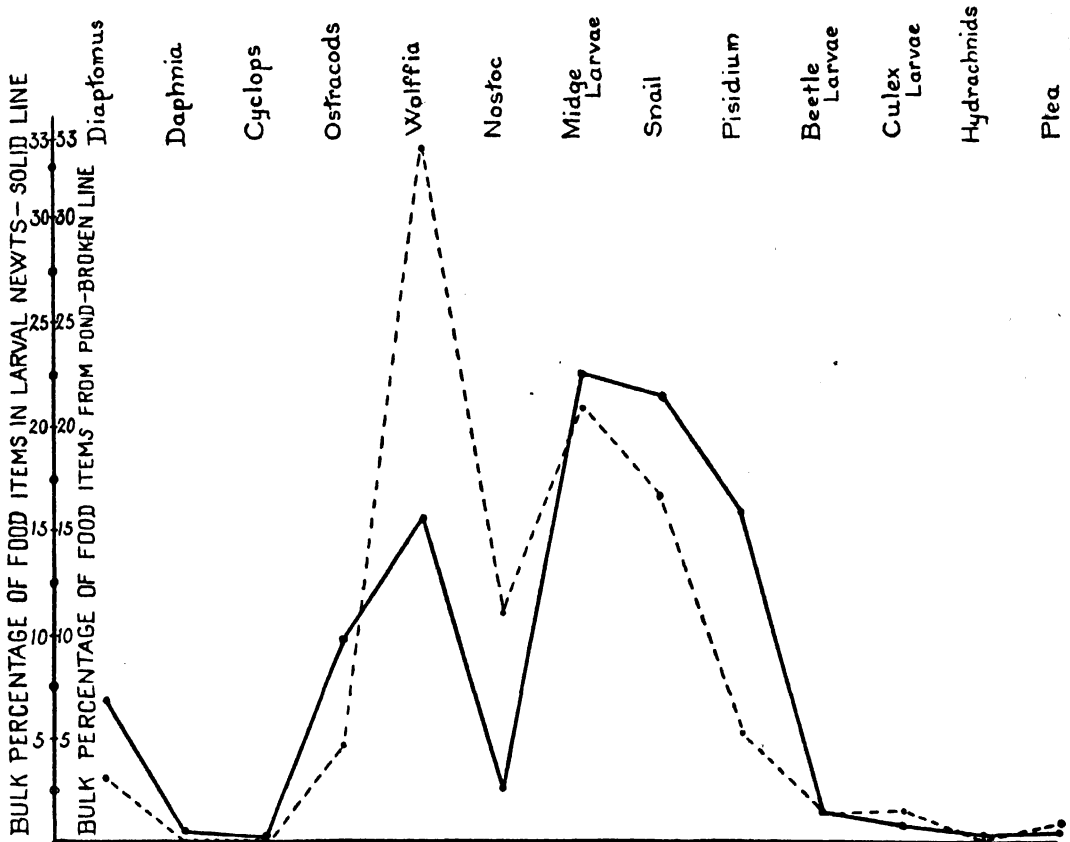
FIG. 2. Relation between prey bulk and bulk of prey items eaten by larval newts. Other than *Wolffia* and *Nostoc*, abundant plants which are probably inadvertently consumed by the carnivorous newts, there is a close correlation between bulk populations and the bulk eaten by newts.

food, and that those prey species which are most numerous will be taken more frequently than the scarcer individuals. In fig. 2 the greatest discrepancy between the bulk of certain food organisms and that contained in the stomachs is to be found among the plants, i.e., *Wolffia* and the small gelatinous colonies of *Nostoc*. This discrepancy can be explained on the basis of feeding habits. Newts are primarily carnivorous creatures and restrict their feeding largely to animals. If the two forms mentioned above had not been so extraordinarily abundant, particularly *Wolffia*, it is probable that few of these would have been ingested. The writer believes that most of the *Wolffia* specimens were inadvertently swallowed by the newts, who took these plants when feed-

ing on small animal life secreted among them.

The experiment does indicate with some certainty that larval *Triturus* feed upon the most abundant species, even when there is a large assortment of foods upon which predilection might be exercised.

## SUMMARY

The present study was designed to determine whether predilection or availability determine the food habits of one wild animal in its natural surroundings. Three hundred larval newts were taken from a pond where a similar number of large prey samples were collected. The resulting data indicate that the newts feed upon small macroscopic organisms in

direct ratio to their availability and accessibility. The study does not suggest that this predator exercises any predilection for certain prey species, or if such does occur, it is not pronounced.

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# CHANGES IN TRUE–PRAIRIE VEGETATION DURING DROUGHT AS DETERMINED BY LIST QUADRATS

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The drought of 1934 was not only the most severe on record for the true-prairie association but was also of the earliest inception. On June 8, Kincer ('34) stated that "pastures are the poorest ever known, and the hay crop will be extremely short, regardless of future weather." The stress increased as the summer advanced. Stoddart ('35) took advantage of these conditions to investigate the relation of osmotic pressure and water content of prairie plants to environmental factors in the vicinity of Lincoln, Nebraska. Simultaneously, Nedrow ('37) was conducting trenching experiments in his study of the efficiency of absorption at different depths by roots of prairie plants. Three of the four prairie grasses studied delayed their development in direct proportion to the depth at which they were watered. Studies of this drought were extended and correlated by Weaver, Stoddart, and Noll ('35), and by Weaver and Albertson ('36). The latter work extended into the mixed prairie where permanent quadrats had been established before the drought. These workers described in detail the drought injury of 1934 and the increase of certain native grasses, native forbs, and ruderals in 1935.

Following the nearly normal precipitation of 1935, the year 1936 was even hotter and drier than 1934. The two following years were likewise drier than normal as was also 1939 at the time of completion of the present study. Rainfall for the early parts of 1938 and 1939, however, was approximately normal. Weather during May contrasted sharply for the two years. That of 1938 was cool and very wet, while in 1939 May was dry and temperatures were far above normal. Prairie soil near Lincoln had 2 per cent or more available moisture at all depths during the growing season of 1938, until late July when the upper 6 inches dried below this point. Sampling in 1939 showed that moisture became unavailable in the first 6 inches as early as May at three stations and at only one was the soil again wet to as much as 20 per cent available moisture in the growing season. The southwesternmost station (Montrose, Kansas) contained no available moisture between the one- and six-foot levels from May to August, inclusive (Weaver and Albertson, '40). Fortunately, a record of the normal condition of the true-prairie association was made just prior to the drought (Weaver and Fitzpatrick, '34).

In 1936, nine prairies which had been described by Weaver and Albertson ('36) were selected for more intensive study of the behavior of true-prairie vegetation following drought. These prairies were within a radius of 110 miles to the south and west of Lincoln. One hundred permanent sample plots, usually one square square meter in area, were located so as to obtain replicate samples of the most important species on each prairie. A census of these was made in 1936 and 1937. The analysis with supplementary studies is published elsewhere (Robertson, '39).

Because of the increasing weediness of the easternmost prairies, portions of several were placed under cultivation in 1938 or 1939, so that only 75 of the sample plots remained. A census of these was taken each summer, and an interpretation of the data is presented here in comparison with that obtained from the same plots in 1936 and 1937.

These 75 plots contained an aggregate of 110 species which included 28 perennial grasses, 40 perennial native forbs, 11 annual native forbs, 1 annual native grass,

and 30 ruderals, nearly all of which were annuals. Determinations near Lincoln before and after the drought of 1934 showed a 36 per cent reduction in basal cover on the upland (Weaver and Albertson, '36). Estimates for the area as a whole vary from 40 to 60 per cent reduction. Fluctuations in cover after 1936 are shown by variations in the number of square decimeter units devoid of vegetation each season. In 1936, there were 3.2 bare units per plot. This was followed by an increase of 25.1 per cent in 1937, an 18.1 per cent decrease in 1938, and a 24.1 per cent increase in 1939, or a net increase of 27.2 per cent since 1936. Certain species were found to be quite stable. For example, from 1936 to 1939 *Amorpha canescens* caused only 2 bared units by its death while invading four, although it occurred in 31 of the sample plots. In contrast, *Agropyron smithii* invaded 163 bare units during the three-year period while creating only 61 new ones, and *Andropogon scoparius* left 19 units bare while invading 8. The relative stability of the most important species and their increase or decrease in 1939 in percentage of the number of stems present in 1936 are given in table 1.

For purposes of comparison, the 110 species were separated into three groups: (a) perennial grasses, (b) perennial native forbs, and (c) annuals—including ruderals, native grasses, and non-grasses.

Perennial grasses in 1938 more than recovered their losses of 1937 and by 1939 this group had twice as many stems as in 1936 (fig. 1). This occurred notwithstanding a general reduction of 20 per cent in 1937 and further small decreases of *Andropogon scoparius* and a few minor species in 1938. The chief percentage gains from 1936 to 1939 were made by *Sporobolus cryptandrus* (480 per cent), *Bouteloua gracilis* (328 per cent), *B. curtipendula* (223 per cent), *Sporobolus asper* (146 per cent), and *Carex* spp. (119 per cent). A similar ranking in 1938 placed *Panicum wilcoxianum, Buchloe dactyloides,* and *Agropy-*

TABLE 1. *Percentage change in abundance and relative stability of important species as shown by the number of bare square decimeter units under observation created by death or invaded from 1936 to 1939*

| | Bare units created | Bare units invaded | Percentage change in abundance |
|---|---|---|---|
| **Perennial grasses** | | | |
| *Agropyron smithii* | 61 | 163 | + 89.0 |
| *Andropogon furcatus* | 46 | 59 | − .4 |
| *Andropogon scoparius* | 19 | 8 | − 39.5 |
| *Bouteloua curtipendula* | 49 | 92 | +223.0 |
| *Bouteloua gracilis* | 1? | 19 | +328.3 |
| *Buchloe dactyloides* | 1 | 7 | + 89.2 |
| *Carex* spp. | 24 | 34 | +119.9 |
| *Koeleria cristata* | 58 | 27 | − 58.2 |
| *Panicum scribnerianum* | 40 | 30 | + .6 |
| *Panicum virgatum* | 16 | 12 | − 2.6 |
| *Panicum wilcoxianum* | 28 | 5 | − 93.0 |
| *Poa pratensis* | 50 | 17 | − 5.6 |
| *Sporobolus asper* | 18 | 18 | +146.3 |
| *Sporobolus cryptandrus* | 14 | 15 | +480.4 |
| *Sporobolus heterolepis* | 10 | 9 | + 11.1 |
| *Stipa spartea* | 9 | 9 | − 24.9 |
| **Perennial forbs** | | | |
| *Amorpha canescens* | 2 | 4 | + 7.1 |
| *Aster multiflorus* | 24 | 50 | − 70.4 |
| *Artemisia gnaphalodes* | 10 | 4 | − 97.4 |
| *Callirrhoe alceoides* | 5 | 3 | − 53.6 |
| *Helianthus rigidus* | 1 | 0 | −100.0 |
| *Liatris punctata* | 3 | 3 | − 72.9 |
| *Lithospermum linearifolium* | 7 | 8 | + 3.4 |
| *Oxalis stricta* | 14 | 17 | +364.7 |
| *Solidago glaberrima* | 22 | 11 | − 95.3 |
| **Annuals** | | | |
| *Bromus tectorum* | 11 | 52 | +764.3 |
| *Chenopodium album* | 1 | 2 | +170.0 |
| *Erigeron ramosus* | 48 | 14 | − 83.8 |
| *Festuca octoflora* | 124 | 139 | − 47.5 |
| *Hedeoma hispida* | 8 | 35 | − 50.9 |
| *Hordeum pusillum* | 4 | 5 | +628.0 |
| *Lepidium virginicum* | 25 | 11 | − 89.6 |
| *Plantago purshii* | 25 | 17 | − 48.1 |
| *Salsola pestifer* | 16 | 13 | +1,800.0 |

*ron smithii* in the first three positions. In actual number of stems gained, *Bouteloua gracilis, B. curtipendula,* and *Agropyron smithii* stood first (figs. 2 and 3). Seven of the 16 most abundant perennial grasses had failed by 1939 to recover their losses of 1936. The most important of these were *Andropogon scoparius, Koeleria cristata,* and *Stipa spartea.* Although *Poa pratensis* disappeared from 33 plots and lost over one-half of its density after 1936, by 1939 it had recovered most of its losses. It was present in all but one of the prairies.
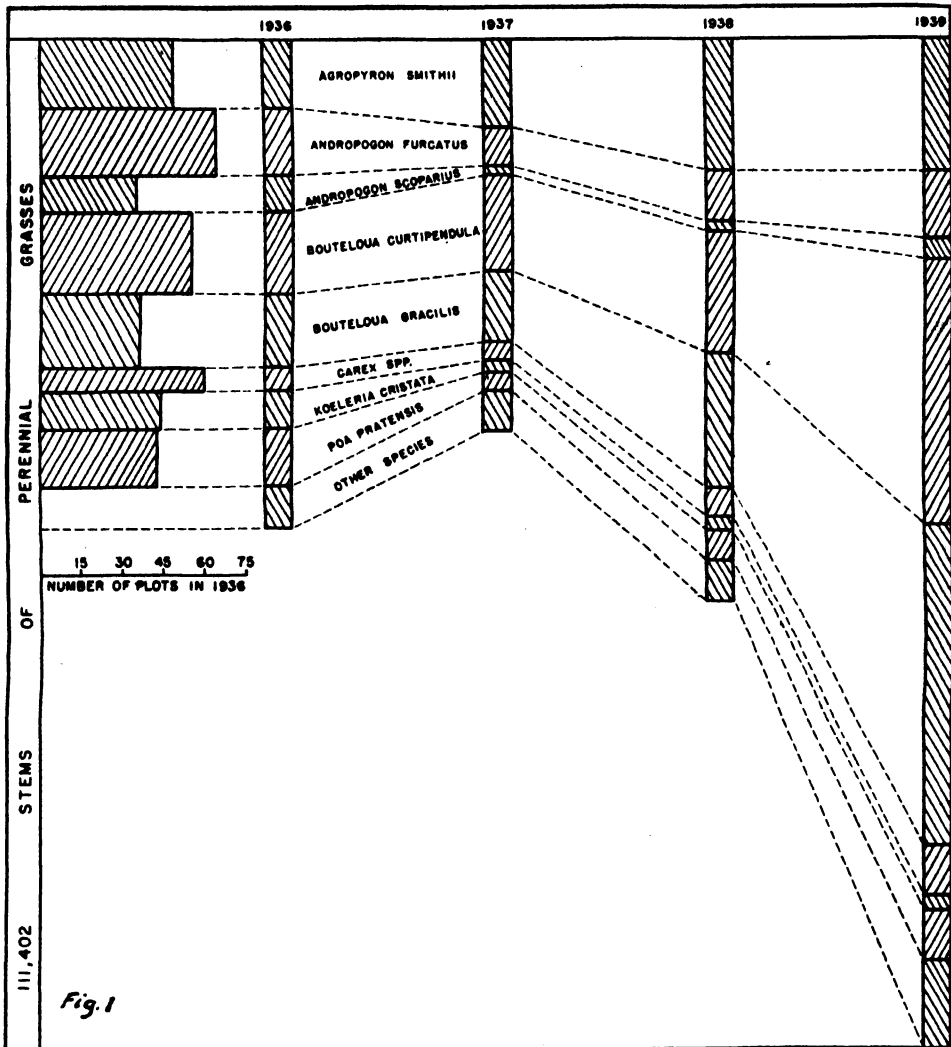
FIG. 1.   Maximum number of stems of perennial grasses, number of plots in which each of the most important species occurred in 1936 (horizontal bars), and relative abundance in the plots (vertical columns) in 1936, 1937, 1938, and 1939.

If the total number of perennial grass stems be taken as 100 for 1936, the values for the three subsequent years are 80, 114, and 205.   No important species decreased its holdings on all of the prairies, and only two (*Bouteloua gracilis* and *Sporobolus asper*) made gains on all the prairies in which they occurred.

Perennial forbs were successively reduced to 72, 53, and 37 per cent of their 1936 abundance in 1937, 1938, and 1939, respectively (fig. 4).   *Aster multiflorus, Artemisia gnaphalodes,* and *Solidago glaberrima* were among the most impor-

tant species to sustain heavy losses. *Oxalis stricta* and *Amorpha canescens* were the only important forbs which made net gains.   No species increased on every prairie, but by 1938 *Achillea occidentalis* had disappeared wherever sampled.   *Artemisia gnaphalodes, Helianthus rigidus,* and *Liatris punctata* all but disappeared.   *Aster multiflorus,* a perennial forb which increased greatly during the drought, had approached normal abundance in 1939.

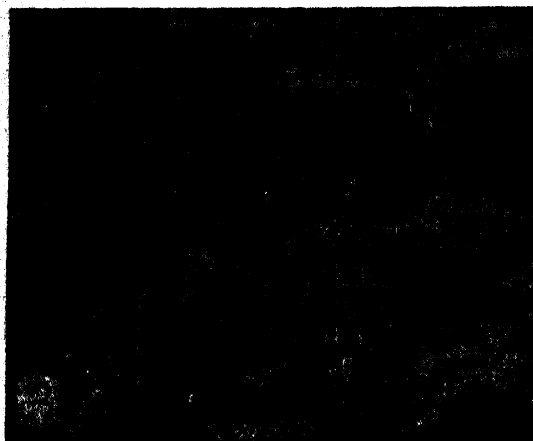Annuals as a group reached their maximum numbers in 1937.   Spring rains

FIG. 2. *Bouteloua gracilis* (light color) spreading in *Andropogon scoparius* prairie. Photo. Lincoln, Nebr., April 29, 1939.

were adequate, the cover was open, perennial grasses were at their lowest ebb, and millions of seeds of all classes of annuals were present. *Festuca octoflora,* a native annual grass, was so abundant and increased so much that it was necessary to abandon the stem-count method and estimate its change by the number of square decimeter units of observation in which it was found each year. On that basis it increased from 1,700 to 2,800 and then to 3,200 square decimeters during the first three years, the gain being



FIG. 3. Portion of a bluestem prairie at Carleton, Nebr., where the former grasses have been almost completely replaced since 1934 by western wheat grass. Note the paucity of forbs. Photo. June 15, 1938.

uniform on the eight prairies where it occurred. In 1939, this annual lost on every prairie it occupied, and entirely disappeared from plots in the eastern stations. *Bromus tectorum* (and closely related species) was the only additional annual to become more abundant in 1938 than in the preceding year. Its gains were somewhat larger on the western prairies, where it invaded several sample plots. Coincident with the rapid increase in perennial grasses, annuals as a group decreased 33 per cent from 1937 to 1938 and 63 per cent from 1938 to 1939. Even so, they were in excess of normal abundance, and perennial native forbs were far below normal. The severe early drought of 1939 was doubtless a cause of the failure of annuals as well as the dwarfing of such early-growing, cool-temperature grasses as *Koeleria cristata, Agropyron smithii,* and *Stipa spartea.*

Of the four years, in 1938 only were seedlings of perennials common. The highest seedling counts were obtained for *Bouteloua curtipendula, Panicum scribnerianum, P. wilcoxianum, Sporobolus asper,* and *Stipa spartea,* in the order named. Only the third and last of these did not show the expected gains the following year. First year seedlings were not included in the census. Among perennial forbs, *Amorpha canescens, Oxalis stricta, Aster multiflorus,* and *Callirrhoe alceoides* had the most seedlings, but none of these survived the drought of the fall and winter.

These findings are in close agreement with those of more generalized surveys and various detailed measurements made annually in these prairies since the inception of the great drought in 1934.

## SUMMARY

A study in nine widely spaced prairies in southeastern Nebraska and north-central Kansas was made by the list, or census, method over the period 1936 to 1939, inclusive. Percentage change in abundance and relative stability of important
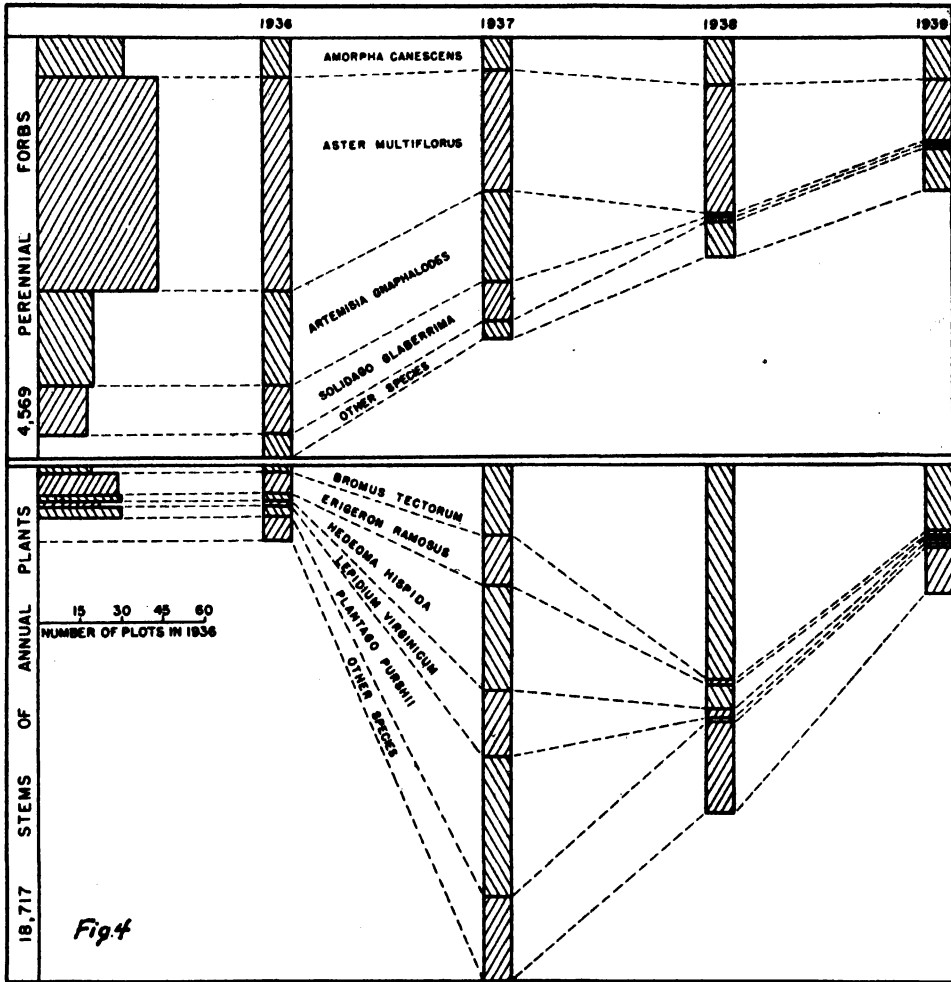
FIG. 4. Maximum number of stems of perennial forbs (upper section) and annual plants (lower section), number of plots in which the most important species occurred in 1936 (horizontal bars), and relative abundance in the plots (vertical columns) in 1936, 1937, 1938, and 1939.

species were calculated from data obtained from 75 plots. A decrease of 20 per cent in perennial grasses and 28 per cent in perennial forbs occurred following the severe drought of 1936.

Perennial forbs continued to decrease until 1939, when they were reduced to only 37 per cent of their 1936 abundance. The greatest losses were those of *Aster multiflorus, Artemisia gnaphalodes,* and *Solidago glaberrima. Amorpha canescens* and *Oxalis stricta* were the only important perennial forbs which made net gains.

Perennial grasses increased in abun-

dance by 1939 to more than twice their abundance in 1936. *Bouteloua gracilis, B. curtipendula,* and *Agropyron smithii,* all xerophytic species, made gains of 328, 223, and 89 per cent, respectively.

Annual plants increased 564 per cent and attained their maximum numbers following the intense drought and great destruction of both perennial grasses and forbs in 1936. *Bromus tectorum* continued to increase until 1938, when it reached a high maximum. As a group, annuals decreased 33 per cent from 1937 to 1938 and 63 per cent from 1938 to 1939.

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# TEN YEARS OF OBSERVATION ON A FRESH–WATER MUSSEL POPULATION [1]

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Because of their economic importance, providing material for the manufacture of pearl buttons, the pearly fresh-water mussels have been studied intensively in this country. The United States Bureau of Fisheries has sponsored many surveys to determine the suitability and productivity of streams for commercial development of mussel fishing and have studied the repopulation of streams that have been depleted by commercial fishing. There have also been some studies on longevity and migration of the Unionidae and the general biology of the group has been admirably rounded out by the studies of the research staff of the Bureau of Fisheries following up the pioneer works of Lefevre and Curtis ('12). However, there are relatively few studies dealing with the status of the Unionidae in a given stream over a long period of time, especially where the stream has been free from exploitation. The writer has had the opportunity of observing the mussel fauna in a small stream over a long period of years where commercial operations would not be profitable and yet where at least twenty-eight species of Unionidae maintain themselves in highly characteristic habitats and in fairly high concentrations of total numbers of individuals.

For more than thirty years the Salt Fork of the Vermilion River at Homer Park, Illinois, has been an outdoor laboratory for classes in Field Zoology in the University of Illinois. Professor Frank Smith conducted regular class excursions to this stream long before the present writer became interested in its mussel fauna.

Prior to 1924, the head waters of this

stream were heavily polluted by the domestic and industrial wastes of the twin cities, Urbana-Champaign, Illinois, part of which were thrown, untreated, into the stream or its branches. With increase in density of population, the contamination became so marked that all of the mussels were exterminated for a distance of about 14 miles below the city of Urbana (Baker, '22). Even during this period of serious contamination the mussel fauna maintained itself in the Homer Park area of the Salt Fork because the distance from the sources of heavy pollution was great enough to permit natural reduction of the load of organic matter. Furthermore, a small dam across the stream near the west margin of the park, where the stream enters, provided aëration to restore oxygen to the depleted water. In 1924, an efficient sewage treatment plant was constructed to relieve the head waters of the Salt Fork. While this has had marked influence on restocking the stream near its source with all forms of life, there are few evidences of modification in the mussel fauna in the Homer Park area.

By exercising care to prevent depletion of the mussels, the same reaches of the stream are studied year after year without any apparent disturbance of the mussel population attributable to the class study. Rather accurate observations have been taken on the relative abundance of the individual species of Unionidae during most of a twenty year period, but for the past ten years records of actual numbers of each species have been kept for each class excursion. Since the trips were all restricted to the last few days of September or the first week in October, the element of variability due to seasonal changes is reduced to a minimum and therefore permits direct comparison of results.

Each class of from 15 to 40 advanced students makes a representative collection of the living mussels. The sampling is not quantitative but characteristic areas are studied on each trip and all the mussels after sorting and enumerating are returned to the stream bed upon completion of the study. Most of the collections are made in water ranging in depth from a few inches to about two feet. Even at these small depths the water is usually too turbid to permit direct observation of the mussels *in situ* in the stream bed. In fact, most of the mussels are located by grappling with the fingers in the gravel, sand and mud, learning to distinguish shells from stones by the feel. Particularly after a summer of drought there are but few of the pools which exceed two feet in depth during the early weeks of fall. Often it is necessary to dig down at least five or six inches to remove some of the larger specimens, many of which are completely beneath the surface of the river bottom. It is seriously doubted if the crow-foot dredges used in commercial operation would bring up specimens from such depth in the mud and gravel.

The writer is fully aware of the fact that hand picking of mussels is not a quantitative method of sampling. The only defense is the fact that the mussels are not uniformly dispersed but show some tendency toward aggregating. Under these circumstances, favorable spots once located yield much larger samples than could be obtained by exhaustive collection of measured areas by quantitative methods. In fact strict quantitative methods are practically inaccessible in the habitat under consideration. On a number of occasions areas of the river bottom have been dug with a shovel and screened through a series of screens. By this method minute specimens of mussels are recovered which are but rarely encountered by hand picking. However this method is effective only in very shallow water and its degree of accuracy is offset by the relative size of the samples avail-

able for study. Similar obstacles preclude the use of bottom samplers which are regularly used in quantitative studies of bottom fauna in larger rivers and lakes. In the Salt Fork, many of the mussels burrow to a depth which cannot be reached by the usual bottom samplers operating in compact sand and gravel. Many collectors, sampling all types of available habitat by random picking of mussels, secure samples which seem to have a fair degree of consistency and permit of comparisons of relative abundance from year to year. As shown later in this paper, statistical analysis of the data throws doubt on the collections as random samples of a population but the source of inconsistency probably lies in the fact that mussels undergo horizontal and vertical migrations between the parts of the stream accessible to collectors and deeper adjacent pools.

In from two to three hours of collecting, several hundred specimens are secured (average, 362), usually representing twenty or more species of Unionidae. By this method of study practically all of the young individuals under three years of age are overlooked and only samples of the mature individuals are taken. Though the object of the study is chiefly a qualitative evaluation of a bottom fauna, the results, because of the size of the samples, are comparable with those of many of the field surveys where critical checks of quantitative methods of sampling are not applied. A similar method of hand picking was employed at least to some extent by operators making reports on the mussel fauna for the United States Bureau of Fisheries (see Wilson and Clark, '14). Danglade ('22) in his report on the mussel resources of the Kentucky River states that the method giving the best results and the one most generally pursued on the head waters "is that of wading and taking the mussels by hand."

Dead shells were not considered in the enumeration of the catch because in many instances these are washed from

other regions in the stream and do not necessarily represent a part of the resident population. Especially in the early years of this study dead shells were in large measure attributable to the serious state of sewage pollution mentioned previously. In high water many dead shells were washed into the study area from locations farther up-stream.

Ordinarily, relatively large samples are accepted as giving evidence of the relative abundance of the organisms in the habitat. Students of natural animal populations very commonly base arguments of change in a fauna on comparisons of samples taken at different dates. In the present study, it is evident that under some conditions the relative abundance of organisms even in fairly characteristic samples may show variations that do not reflect essential changes in the fauna. Methods of sampling and migration of the organisms are possible variable factors which must be given as much attention as the actual relative numbers of individuals in the samples being compared. An analysis of samples of Unionidae covering ten consecutive years (Table I) has shown that in many instances apparent changes in the fauna between two adjacent years are based on faulty sampling or arise from migratory movements of the mussels to or from deeper waters.

Isely ('14) in discussing observations on migration of marked individuals of Unionidae released in streams, called attention to the fact that in water over three feet deep the plantings remained practically stationary, showing little tendency to migrate. On the other hand, those which he placed in shallow water always moved until they reached water 2 to 3 feet deep. Since in late summer the water in the Salt Fork is rarely 3 feet deep except in a few of the deeper pools, it is very probable that for some species active migration is very general at that time.

Coker, Shira, Clark and Howard ('21) have expressed the belief that changes in

water level and in temperature are the most likely factors influencing migration of mussels. In analyzing the possible factors further these same authors state (p. 82), "The reaction to evident stimuli consists merely in closing up; there are times, however, when a mussel is impelled to change its position. The movement may then be in a vertical direction, the mussel going down deeper into the bottom; rarely does it go completely beneath the surface of the bottom; more frequently the mussel moves horizontally, leaving a distinct path behind it, which reveals the direction and distance of travel." . . . "Change of pressure (depth), temperature, or more probably light may be the governing factor."

Evermann and Clark ('18), dealing with a lake habitat, state categorically (p. 250) that, "The mussels in shallow water near the shore move into greater depths at the approach of cold weather in late autumn or early winter and bury themselves more deeply in the sand." They state further that "locomotion of fresh-water mussels can play little part in their distribution." If this interpretation is limited to a consideration of broad geographical dispersal, the present writer is in agreement, but in streams of variable water level, such as the Salt Fork, migration is the only basis on which certain observations of change in numbers are explainable. For instance, the white heel splitter (*Lasmigona complanata*) is an active species. In the collections (Table I) this species comprised 11.2 per cent of the entire sample on September 26, 1933, but fell to 3.6 per cent of the sample taken just one week later. In all of the succeeding years, this species represented approximately 9 per cent of each collection. Since all of the individuals were several years old, a local catastrophe could not explain the reduction in numbers between September 26 and October 3 of the same year when the numbers returned to near normal in the sample taken the following year. The only available explanation of the sudden decrease

in numbers in one week's time in 1933 is that some changed environmental condition induced lateral migration into deeper water or vertical migration to a deeper level in the river bottom. Reference to the Weather Bureau records indicates that a drop of 10° occurred in both maximum and minimum air temperatures for this region between the two dates of collection, with 33° difference between the maximum and minimum air temperatures. In shallow water such sudden changes might readily bring about migratory movements toward deeper water.

Of the 28 species encountered in the restricted region of this study in the past ten years, only three have occurred regularly in a relative abundance that exceeds 10 per cent of the take, and in fluctuations from year to year these show no consistent trend in relative numbers among themselves. *Lampsilis ventricosa* has averaged the highest in relative frequency throughout the ten years (14.36 per cent) but in the past two years it has declined slightly and in relative abundance it has been surpassed by *Tritogonia verrucosa*. Burrowing deeply into the hard-packed gravel, *Lampsilis ventricosa* is apparently little influenced by environmental factors of temperature, light, and pressure. Because of its sendentary habits, it might be assumed that this species would be disturbed in its habitat relations by the frequent digging out of large numbers of individuals and returning them to the stream where they are forced to reëstablish themselves. Evidently this presents no serious hazards to this species because the numbers have shown little fluctuation

TABLE I. *Eleven collections of Unionidae from the Salt Fork at Homer Park, Illinois during a ten year period, 1930 to 1939. For each date the relative abundance of each species is expressed in per cent of the entire collection for that date*

| | Sept. 30 1930 | Sept. 29 1931 | Sept. 29 1932 | Sept. 26 1933 | Oct. 3 1933 | Sept. 27 1934 | Oct. 3 1935 | Oct. 6 1936 | Oct. 5 1937 | Oct. 4 1938 | Oct. 3 1939 | Average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total individuals in sample | 439 | 509 | 449 | 412 | 419 | 301 | 126 | 215 | 263 | 528 | 325 | 362 |
| *Lampsilis ventricosa* | 14.8 | 9.8 | 18.9 | 12.4 | 15.0 | 13.3 | 13.5 | 16.3 | 17.1 | 14.2 | 12.6 | 14.36 |
| *Tritogonia verrucosa* | 10.9 | 9.4 | 9.4 | 9.7 | 9.6 | 4.3 | 7.9 | 7.9 | 14.5 | 16.3 | 17.9 | 10.70 |
| *Lasmigona complanata* | 14.1 | 9.2 | 12.7 | 11.2 | 3.6 | 9.0 | 11.9 | 8.8 | 11.0 | 10.2 | 14.2 | 10.54 |
| *Fusconaia flava* | 3.9 | 3.6 | 5.1 | 9.2 | 14.3 | 10.0 | 13.5 | 10.2 | 10.3 | 10.4 | 7.4 | 8.89 |
| *Quadrula pustulosa* | 6.8 | 7.5 | 7.6 | 6.3 | 15.3 | 9.3 | 4.8 | 9.8 | 7.6 | 11.8 | 7.4 | 8.54 |
| *Amblema costata* | 6.2 | 4.7 | 6.0 | 12.1 | 9.8 | 4.3 | 6.4 | 5.1 | 5.3 | 6.4 | 10.2 | 6.95 |
| *Lampsilis siliquoidea* | 5.5 | 7.1 | 5.6 | 9.0 | 2.9 | 5.7 | 7.9 | 8.4 | 2.3 | 2.1 | 3.4 | 5.42 |
| *Cyclonaias tuberculata* | 1.6 | 4.9 | 3.1 | 2.9 | 6.7 | 6.3 | 2.4 | 3.7 | 8.0 | 6.8 | 6.8 | 4.84 |
| *Actinonaias carinata* | 3.0 | 5.3 | 2.0 | 2.4 | 2.6 | 9.3 | 5.6 | 5.6 | 4.6 | 6.1 | 6.8 | 4.83 |
| *Lampsilis fasciola* | 3.0 | 6.1 | 4.0 | 4.6 | 6.7 | 6.6 | 4.0 | 2.8 | 7.2 | 2.8 | 1.5 | 4.49 |
| *Pleurobema coccineum* | 2.7 | 5.5 | 6.5 | 4.4 | 3.3 | 3.3 | 2.4 | 6.1 | 2.3 | 4.2 | 3.7 | 4.03 |
| *Lasmigona costata* | 10.3 | 7.9 | 7.6 | 1.7 | 2.4 | 4.0 | 0.8 | 3.3 | 2.3 | 3.0 | 1.2 | 4.03 |
| *Anodonta grandis* | 1.6 | 4.1 | 2.9 | 1.9 | 2.2 | 9.3 | 10.3 | 6.5 | 2.3 | 0.6 | 0.3 | 3.82 |
| *Strophitus rugosus* | 4.8 | 4.3 | 2.7 | 4.6 | 1.9 | 2.3 | 3.2 | 1.4 | 1.9 | 1.9 | 1.9 | 2.80 |
| *Alasmidonta marginata* | 4.3 | 4.1 | 2.2 | 4.1 | 1.9 | 1.3 | | 0.5 | 0.8 | 1.0 | 3.1 | 2.12 |
| *Ligumia lienosa* | 2.7 | 1.8 | 1.3 | 1.0 | 0.2 | 0.3 | 1.6 | 0.5 | 0.8 | 0.4 | | 0.96 |
| *Quadrula metanevra* | 1.1 | 3.3 | | 0.2 | 1.2 | 0.3 | 1.6 | 0.9 | 0.4 | 0.4 | 0.9 | 0.95 |
| *Ligumia iris novieboraci* | 0.2 | 0.2 | 1.3 | 1.0 | 0.5 | 0.3 | | 0.5 | 0.4 | 0.4 | 0.3 | 0.46 |
| *Carunculina parva* | 1.4 | 0.2 | 0.2 | 0.2 | | 0.3 | 0.8 | 0.5 | 0.8 | 0.2 | 0.3 | 0.44 |
| *Quadrula quadrula* | | 0.6 | 0.2 | 0.2 | | | 1.6 | | | 0.6 | 0.3 | 0.32 |
| *Pleurobema clava* | 0.7 | 0.2 | 0.2 | 0.2 | | | | 0.5 | | 0.2 | | 0.18 |
| *Ligumia ellipsiformis* | | | | | | 0.3 | | 0.5 | | | | 0.071 |
| *Uniomerus tetralasmus* | 0.2 | | | 0.2 | 0.2 | | | | | | | 0.064 |
| *Anodonta imbecilis* | | | | | | | | | 0.5 | 0.2 | | 0.059 |
| *Carunculina glans* | 0.2 | | | 0.2 | | | | | | | | 0.04 |
| *Quadrula cylindrica* | | | | | | | | | | 0.4 | | 0.035 |
| *Obovaria subrotunda* | | | | | 0.2 | | | | | | | 0.021 |
| *Lasmigona compressa* | | 0.2 | | | | | | | | | | 0.02 |

even though the species has been subjected to human disturbance for a period well over 30 years without any apparent influence on its relative abundance in the habitat.

*Tritogonia verrucosa* and *Lasmigona complanata* in contrast with the foregoing species are relatively active wanderers. As previously noted, this is reflected particularly in the collections of *L. complanata* where in two collections a week apart the number fell from 11.2 per cent to 3.6 per cent in the samples. Had active horizontal migration not been operating the transplanted sample of the earlier date should have tended toward producing a higher yield of individuals readily accessible on the surface of the river bottom on the second sampling trip. Aside from the vagaries of sampling, *Tritogonia verrucosa* shows evidence of distinct fluctuations in abundance, having progressively reached a low in 1934 and then progressively ascended to an all time high in 1939. For two years *T. verrucosa* has replaced *L. ventricosa* as the most abundant species in the habitat.

In contrast, *Lasmigona complanata* has varied through a range of 3.6 per cent to 14.2 per cent but in the ten years this variation is apparently meaningless so far as actual cyclic abundance is concerned. The apparent low in 1933 has already been explained as undoubtedly traceable to horizontal migration, reflecting no actual change in numbers. There is unconvincing evidence of fluctuating diminution in numbers from 1930 to 1934 followed by a subsequent slight increase to the present, but on the whole the fluctuations seem wholly fortuitous and attributable to errors in sampling complicated by active translocation of individuals.

Especially among the thin-shelled species there are evidences of progressive diminution in numbers over the ten year period. *Lasmigona costata, Lampsilis siliquoidea, Anodonta grandis, Strophitus rugosus, Ligumia lienosa,* and *Alasmi-*

*donta marginata* have appeared consistently enough in the samples to warrant the generalization that numbers are in actual decline for these species and that the reduced numbers are not due to the technique of sampling. Not all the contributory causes are evident but at least one factor has been observed. In 1935, the workings of muskrats became so conspicuous in the area that a memorandum was entered in the field notes. Three 12-quart pails of empty shells were taken from a pile at the mouth of a single muskrat working. Most of these were of the thin-shelled varieties, such as those mentioned at the opening of this paragraph. Not all of the species showed the same response to the predation of the muskrat. *Anodonta grandis,* which was in that year on the crest of a distinct increase, did not reflect the decline until the following year but the complex of factors operating on this species have continued to deplete the numbers until in the last two years this species has been represented by less than 1 per cent in the samples. *Lasmigona costata* and *Strophitus rugosus,* already in decline when the effects of the muskrat predation became obvious, have never regained their former abundance, but as active migrants their numbers have fluctuated considerably in the samples. *Alasmidonta marginata* disappeared entirely in 1935 but has since increased progressively, though at least in some measure the increase in numbers of this species may be due to migration into the easily available collecting grounds from deeper adjacent pools rather than to normal reproductive processes.

After 1935 the direct effects of muskrats have become less obvious. Fewer slides have been observed and the dead shells encountered have been scattered instead of forming compact heaps at the mouth of burrows.

Eleven of the 28 species of Unionidae would be classed as rare or infrequent in the community under consideration,

rarely attaining a prominence above 1 per cent of the total sample. Several of these have small shells and hence escape the collector. Most of them have high dispersal at low frequency throughout the habitat, and since some are known to be relatively more abundant farther down the same stream, the area under consid- eration seems to represent the frayed margin of their limits of distribution. The limits to dispersal of such species seem to be very complicated. Proper physical environment for the adult mus- sel, important as it may be, is only one of a series of factors in which the dispersal of the fish hosts seems to be even more significant. From an area of dense popu- lation of one of these rare species, a fish host with transforming glochidia wanders into new territory shedding juvenile mus- sels beyond the usual bounds of the spe- cies. Unless physical conditions elim- inate these outposts of the species the distribution becomes extended in a fringe of low intensity.

There have been a few significant ob- servations on relative numbers extending over a period of time greater than the ten years for which actual numbers of individual species are available. In 1926, Tucker ('27) found part of her supply of *Anodonta imbecilis* in the immediate stretches of the stream under considera- tion but in the past ten years this species has been lacking in all but two of the samples when a single specimen was taken in each instance, though dead shells are often encountered.

Baker, in 1922, published the results of several years of study of the mol- luscan life of the Salt Fork. Though he gave the results in terms of relative abun- dance, it is evident that the local status of some of the species has changed in the intervening time. He reported *Ano- donta imbecilis* as common. *Lampsilis anodontoides*, which he found infrequent in the mud, has been wholly missing for at least ten years. Of *Obovaria subro- tunda*, reported as infrequent in 1922, a

single specimen has been observed in the past ten years. *Ligumia iris novieboraci*, lacking in 1922, has been fairly uniformly represented by small numbers more re- cently. *Actinonaias carinata*, found in- frequently by Baker, has been progres- sively on the increase until from 6 per cent to 9 per cent of recent collections have been of this species.

In the restricted area of the Salt Fork under direct consideration the relative and absolute numbers of each species is de- termined by a complex variable out of which certain species maintain them- selves at a fairly constant level, while others at the same time show fluctuations in numbers often indicating progressive increase or decrease independently for the individual species. One form may be in decline while another is becoming more abundant.

Sudden changes, involving conspicuous increases or decreases, which are not con- sistent trends are attributable to faulty sampling or to localized population shifts due to immigration or emigration from waters of different depths. Species differ widely in their response to factors induc- ing migratory movements. Water level and temperature changes seem to be the most readily available bases for explain- ing migratory movements affecting tem- porary shifts in population.

Predation is an important factor in de- termining the population, especially among thin-shelled species living in shallow water but species in different phases of cyclic abundance show different reaction time in reflecting the effects of predation.

Evidences for faunal changes in studies of the Unionidae even when based on sev- eral years of observation must be checked against the possibility of inaccuracy in sampling methods and unreliability of in- dividual samples influenced by differential migratory movements of the individual species.

In an attempt at statistical analysis of this series of collections Dr. Lester Ingle has very kindly prepared Table II from the original data.

TABLE II. *Statistical analysis of characteristic species of Unionidae from the Salt Fork at Homer Park, Illinois*

| Species | Mean | Standard Deviation | Standard Error |
|---|---|---|---|
| Lampsilis ventricosa | 51.5 | 18.5 | 5.86 |
| Fusconaia flava | 30.1 | 14.2 | 4.50 |
| Tritogonia verrucosa | 40.0 | 20.5 | 6.50 |
| Lasmigona complanata | 38.0 | 16.4 | 5.20 |
| Quadrula pustulosa | 32.1 | 16.5 | 5.20 |
| Strophitus rugosus pavonius | 10.64 | 6.8 | 2.10 |
| Quadrula quadrula | 1.83 | 0.9 | 0.37 |

From this table, certain facts are obvious. Thus in the instance of *Lampsilis ventricosa,* when the series of samples is analyzed, if the samples were random and the population had not varied significantly, 95 out of 100 cases should fall within the limit of twice the standard error on each side of the mean. Under this condition the collections should fall between an upper limit of 63.22 and a lower limit of 39.78. Five of the 11 cases fall outside these limits. It therefore seems obvious that in these samples we are not dealing with a stable population but with samples influenced by factors disturbing uniform horizontal and seasonal distribution of individuals.

The collections of the individual species lack consistency in numbers that might be expected from a stable population in which the life span of the individual covers several years with distinctive growth forms. Environmental changes causing decimation or speeding reproductive rate cannot influence a given sample without being reflected immediately in succeeding samples. In this regard species having a life cycle of several years duration differ from forms with a short life cycle that enables intercalated reproductive cycles to materially alter the population between samples.

## SUMMARY

1. Twenty-eight species of Unionidae in the Salt Fork River at Homer Park, Illinois have been under observation for about 20 years with definite records of sampling available for 10 years. Because strictly quantitative methods could not be applied, the samples were taken by hand picking from the stream bed.

2. While some species have showed marked changes in their relative status in the area under consideration, many have maintained themselves in fairly consistent numbers and few species have given evidence of definite trends of significant changes in relative abundance.

3. Sudden changes in numbers not reflected in successive samples must be attributed to factors other than population changes because the length of life span is too great to permit repopulation between successive sampling dates.

4. Some species irregularly represented in the habitat are at the frayed margin of limits of their distribution. Dispersal of the essential fish hosts in the stream is probably just as important as presence of suitable environmental conditions for the mussels in determining the distribution of these forms.

5. Statistical analysis of the data shows that the samples of individual species are not samples of a stable population. Since length of the reproductive cycle precludes the possibility of repopulating between collecting dates migration is pointed out as the most likely factor responsible for inconsistency of the samples.

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# ECOLOGICAL COLOR VARIATION IN A BUTTERFLY AND THE PROBLEM OF " PROTECTIVE COLORATION "

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The distribution area of *Oeneis chryxus* Dbld. & Hew. (Lepidoptera: Satyridae) extends from the arctic regions of North America, south through the high ranges of the Rocky Mountains, the Sierra Nevada and the Great Basin as far south as New Mexico. The butterfly is not uniformly distributed over this area but is found only in the Arctic-alpine life-zone and in the unforested ridges of the upper Hudsonian; hence, in the southern parts of its range, it is restricted to isolated "islands" on the higher peaks. The species is variable with respect to the predominant color on the upper surfaces of the wings, some individuals being a rather dark yellow-brown, others a medium yellow-brown and in extreme instances, yellow-white. The colors appear to be entirely quantitative in nature; individuals showing all different intermediate shades of color can be arranged from darkest to lightest. Within a restricted population, however, the individuals are remarkably uniform and only very occasionally are atypical examples found. Most populations consist of individuals of a rather dark yellow-brown color; occasional ones consist of extremely light or extremely dark forms.

In California and western Nevada, the species is represented by two races, a very pale, yellow-white race (*ivallda* Mead, fig. 5*B*) and a very dark, yellow-brown race (*stanislaus* Hov., fig. 5*D*). The distribution area of each of these races is shown on the map (fig. 1); the localities where the white race has been found are shown by circles and those of the brown race by triangles. The contour line shown on the map approximately encloses the habitable territory of the species, this being the Arctic-alpine and upper Hudsonian life-zones. The color shade of individuals inhabiting the various locali-

ties is shown on the diagram (fig. 2). The horizontal scale indicates the geographical position of the locality while the vertical scale indicates the shade of color, darkest at the top and lightest at the bottom; the line connecting the points gives an index of the steepness of the variation gradient (*cline* as used by Huxley, '39) between the localities. At Sonora Pass, in the center of the range of the brown race, white or light-colored individuals are taken very rarely. Between Ebett and Echo Passes the populations all lighter in color, but entirely white individuals are as yet unknown. South of Sonora Pass to a point north of Tioga Pass where the brown and white races appear to interbreed, the population of the brown race is nevertheless dark, showing no variation gradient. In the very narrow transition zone, however, the population is mixed, showing the entire range of variation from the darkest to the lightest. These facts would seem to indicate that the differences between the brown and white races are not due to a single gene, but rather to a combination of several genetic factors, and that these factors or genes are widely distributed throughout the entire range of the species though with differential concentrations. As far as one can judge without genetical experimentation, the white races from the northern and southern sections are entirely identical even though the intervening area inhabited by the dark race is at least eighty miles in extent. The shortest means of communication between the two regions is through that occupied by the brown one (fig. 1). Furthermore, as the surrounding territory is of lower elevation and is in a different life-zone, it is ecologically unsuited for the existence of this particular species; it could hardly be a region through which migration could
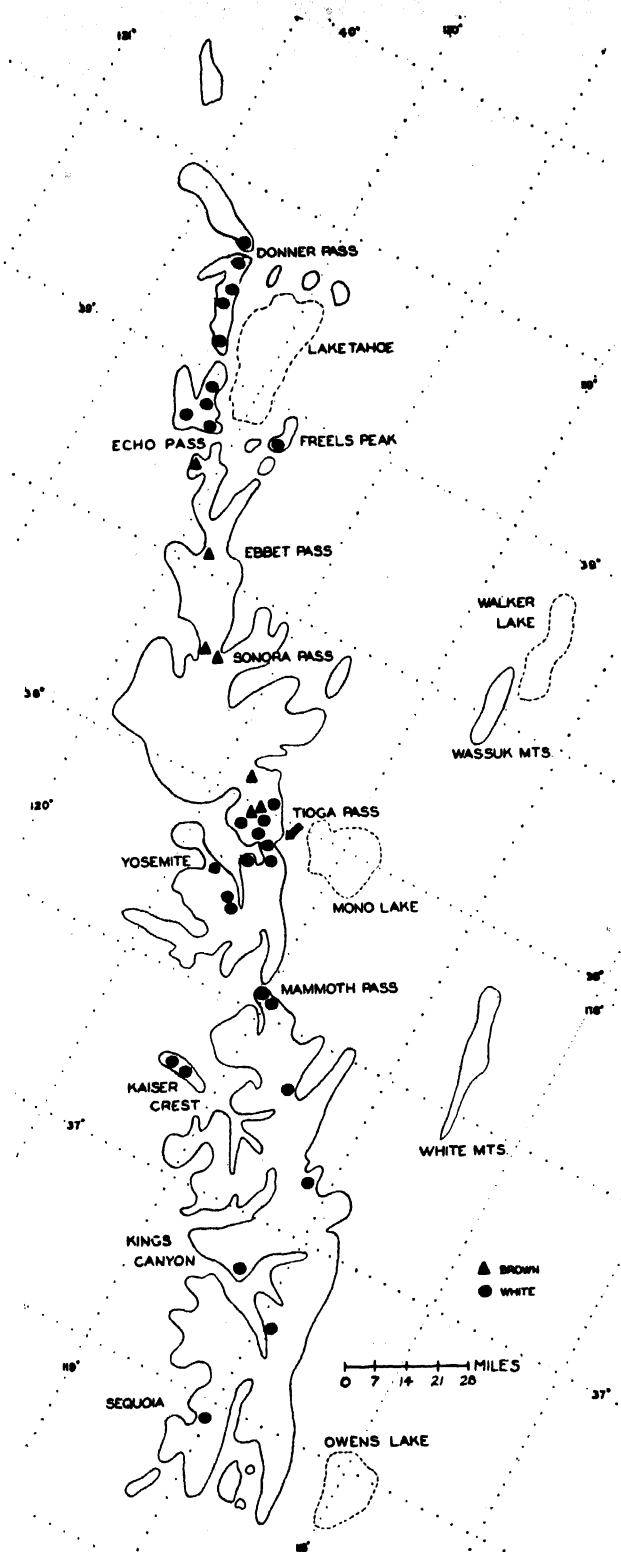
Fig. 1. Map showing extent of Arctic-alpine and upper Hudsonian life-zones in the Sierra Nevada of California and the mountains of western Nevada. Localities where *O. chryxus ivallda* has been recorded are designated by a circle and those of *O. chryxus stanislaus* by a triangle.
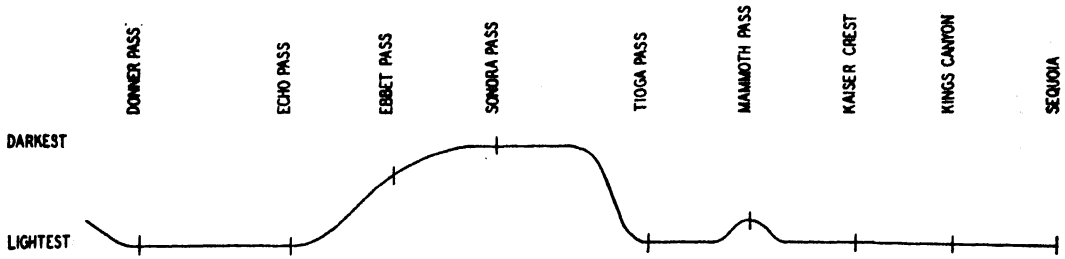
FIG. 2. Diagram showing the shade of yellow-brown coloration typical for populations of *Oeneis chryxus* at various localities in the Sierra Nevada. The data from which this is derived were not photometrically studied (because of the lack of facilities) nor compared with a set of color standards (because the correct shade and tints were unobtainable); comparisons were made with arbitrary standards of the material itself. The diagram is, therefore, not to be taken too exactly.

take place. That is the status of the variation, but what is the origin of the color races and what are the reasons for their present distribution?

### ORIGIN OF THE COLOR RACES

A discussion of the origin of the color races can only be speculative and theoretical, but the evidence available does allow one to comment upon several alternatives. It may be postulated: (1) That the Sierra Nevada was once entirely populated by a white race and that the brown race has either originated *de novo* in the central part or that it has come in via the high Basin Ranges from other populations of the brown form; (2) That the Sierra Nevada was once populated entirely by a brown race at either end of which genes for whiteness developed greater concentrations, or (3) That a uniform population never did exist in the Sierra Nevada. A discussion concerning these could not be conclusive when there is a total lack of paleontological evidence, but some pertinent information can be given. For example,

*A.* No other populations of white individuals exist in any part of the range of *Oeneis chryxus* and yet the two identical white races exist isolated from each other at the present time in the Sierra Nevada.

*B.* The light and dark races are interfertile and interbreed on the borders of their ranges, at which places intermediate

individuals are produced. Continued interbreeding over a period of years should tend to eliminate the differences between them and produce a uniform, intermediate-colored population.

*C.* No other white races exist which would tend, by migratory individuals, to increase the concentration of white-producing genes in the northern and southern Sierra Nevada. Other brown races do exist which could increase the concentration of brown-producing genes. Individuals from these populations (in the Rocky Mountains) could more easily reach the Sierra Nevada via the high Basin Ranges which form a series of "stepping-stones" across the uninhabitable desert areas of that region than via any other way. These are most numerous in the region directly east of the central Sierra Nevada at Sonora Pass. Other things being equal, were the influx of brown-producing genes sufficient to produce this central, brown race in the first place, it should be sufficient to change the entire Sierra Nevada populations into a single brown race.

One is forced, therefore, to ask the following questions: If the brown-producing genes have gained in concentration without the external help of migrations, what factors have allowed this increase over white-producing genes or vice versa, if the white-producing genes have gained in concentration without the external help of migrations (and it is definitely impossible

to do otherwise in this case), what factors have allowed this increase over the brown-producing genes? Also, if the brown-producing genes have gained in concentration *with* the aid of migrations, what factors have prevented further spread into the regions now with greatest concentration of white-producing genes? If a uniform population never existed in the Sierra Nevada, what factors have prevented such a uniformity from becoming established and what has been the causal agent of the specific distributions observed?

### REASONS FOR THE OBSERVED DISTRIBUTION

As a result of the evidence above, it can only be assumed that selection of some sort has been operative in producing the observed distributions of the white and brown races. The problem is to find the differential factors allowing for selection and then to find the specific mechanism of selection. All the possible factors which have been thought to have any bearing on selection may be placed under one of these three groups: differences in the climate, the food or the habitat. The first, climate, is not likely to be such a factor because within the Sierra Nevada, the white and the brown races inhabit the same life-zone and the white race lives both north and south of the brown race (humidity decreases southward). It may be assumed that there is no difference in general climate affecting the selection of one race in preference to the other, except wherein this may be due to some other factor indirectly. The second group, food, is likewise probably not a factor because as far as the information is available at present, the food plants of the larvae of both races are the same, namely, species of alpine grasses; more data on this subject, of course, is needed. Only in the third group, habitat, can we find a striking difference in the environment of the two races; this is in the color of the ground rock, which is the most obvious feature of the landscape above timberline

(figs. 3 and 4). Soil cover at the elevations where *Oeneis chryxus* lives is scarce, and the alpine meadows where there is any considerable amount are unsuitable as a habitat. The insect lives almost exclusively on rocky terrain and the rocks, rather than plants or soil, give the predominant color to the landscape. The rock in the northern and southern Sierra Nevada, where the white race is found, is predominantly a white granite (fig. 5A). On the contrary, in the distribution area of the brown race, the central region, the mountain tops are composed of dark red rocks (fig. 5C). Jenkins ('38) and personal observations show that the country above timberline from Echo Pass to a point south of Sonora Pass is composed mostly of dark-red Tertiary volcanics and of red Miocene andesite. North of Echo Pass, as well as in a greater part of the range above timberline from north of Tioga south to Sequoia, a very light-colored Jurassic granite is decidedly predominant. The accompanying photographs (figs. 3 and 4) illustrate the characteristic difference in the coloring of the landscape. The distribution map (fig. 1) shows that the ranges of the brown and white races almost exactly coincide with the distribution of the different kinds of rock. The presence of the more gradual gradient (fig. 2) at the northern part of the brown races' distribution can be explained by the fact that in this region there is a decreasing percentage of dark rock in relation to the light as one proceeds northward. To the south, the change is more abrupt. The "humps" seen in the diagram are also explained on the same basis; areas of dark rock are of increasing abundance in these regions.

Since the relation between the color of the butterfly and the color of the rock is the only relationship observed, the cause or mechanism of the selective effect must be found. Two possibilities are open, namely, selection by predators or selection by physiological fitness for the environment. If selection by predators is in-
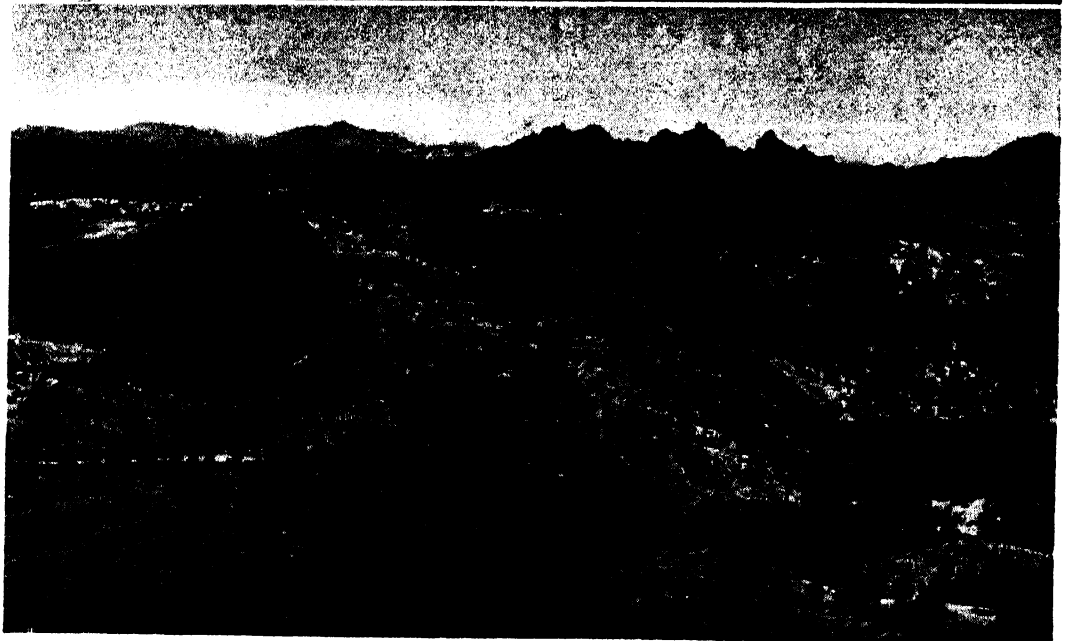
FIG. 3.   High Sierra Nevada in the Yosemite-Tioga Pass region showing the granitic aspect of the country at timberline where the white race occurs.

FIG. 4.   High Sierra Nevada in the Ebbet Pass region showing the dark, volcanic aspect of the country at timberline where the brown race occurs.

volved, one must first be able to find the predators and second, one must be able to discover that the protective color is really an aid in concealment from these predators. These requirements are seldom fulfilled in the very voluminous literature dealing with real or supposed protective coloration or mimicry. Even some most recent writers have not done

this (*e.g.* Dice and Blossom '37; Benson '33) but appear merely to have assumed that the correlation between the coloration of some races of mammals and that of the ground on which they live is due to protection from predators. The actual proof of selection by predators (or by any other means) on any living thing in nature has not yet been shown; in fact,
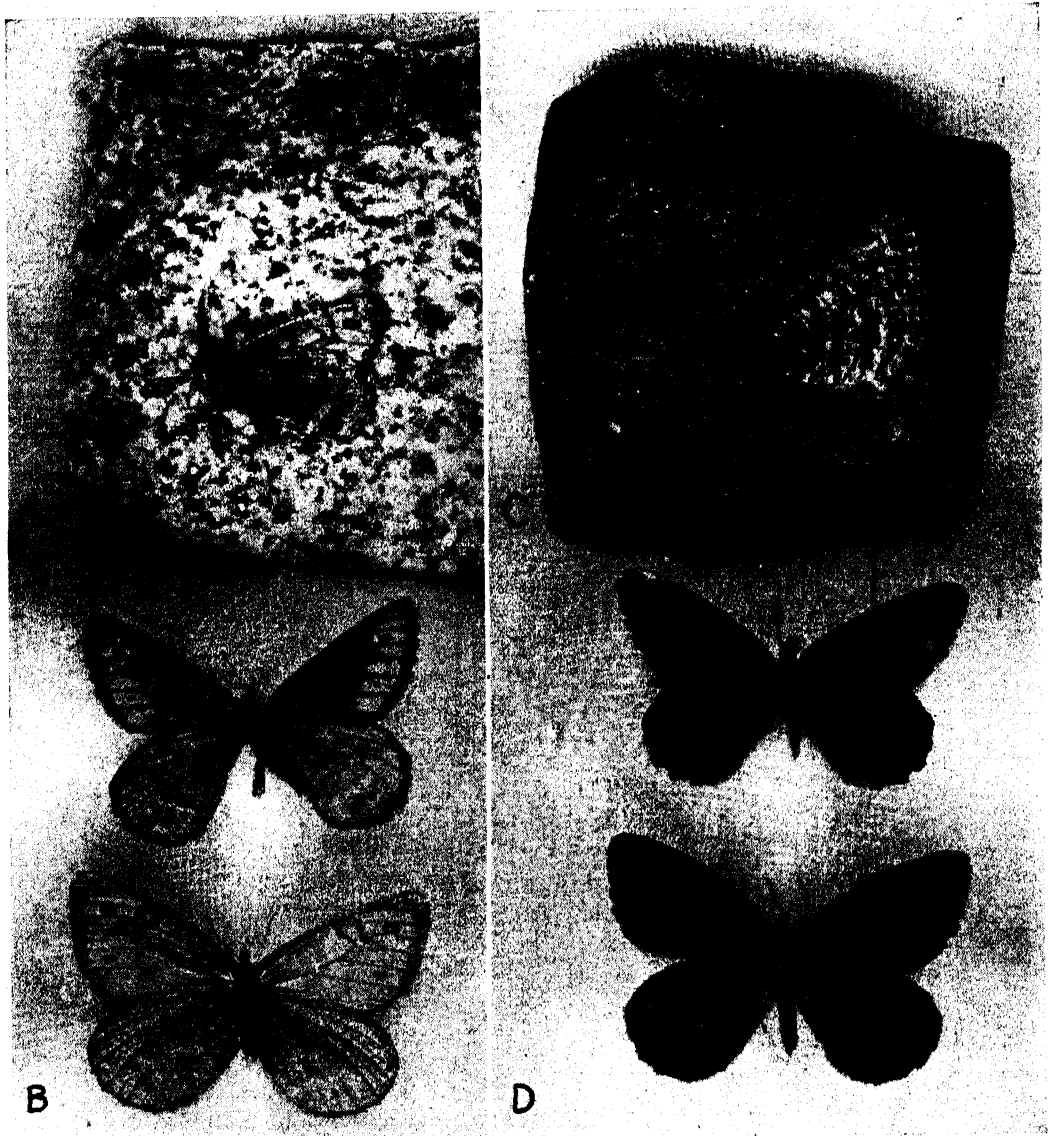


FIG. 5. (*A*) A granitic rock and a specimen of the white race with the wings closed. (*B*) Upper surfaces of *Oeneis chryxus ivallda* showing the predominately white color. Top specimen is a male and the bottom one is a female. (*C*) An andesite rock and a specimen of the dark race with wings closed. (*D*) Upper surfaces of *Oeneis chryxus stanislaus* showing the predominately darker color. Top specimen is a male and the bottom one is a female.

in most cases of supposed protection by protective resemblance, it has never been shown that the actual effective natural predator is selective on account of the supposed protection. Shull ('37) states that it is not up to the opponents of the mimicry theory to disprove the statements of the proponents, but rather the latter must present experimental evidence in favor of it first. Dobzhansky ('37; p. 164) states: "Taken as a whole, an unprejudiced observer must, I think, conclude that an experimental foundation for the theory of protective resemblance is practically non-existent." The experiments of di Cesnola ('04), Beljajeff ('27), Sumner ('35), Carrick ('36), Isely ('38), Reighard ('08) and others were conducted to prove or disprove whether cryptic or warning coloration is a factor of differential selection of prey by predators. Some of these have proven that cryptic coloration gives a selective advantage to the posessor of this coloration under the artificial conditions of predator pressure prevailing when and where the experiments were carried out, and at most can only be suggestive of wider implications. Whether or not the prey is under such predator pressure in nature and whether or not such "protective" coloration is effective or necessary under these conditions is another thing to be proven; certainly the prey must be allowed to protect itself by its own specific habits and mode of living. Heikertinger ('33–'36) and McAtee ('32) have criticized the mimicry theory rather thoroughly but neither's evidence is sufficient or convincing enough to be effective. Pearl ('30) states as the basic and minimal requisites of an observational or experimental demonstration that natural selection has altered a race in any particular instance the following: "*A*. Proof of somatic difference between survivors and eliminated. *B*. Proof of genetic differences between survivors and eliminated. *C*. Proof of effective time of elimination. *D*. Proof of somatic alteration of race. *E*. Proof

of genetic alteration of race." No author has yet satisfied these, nor has anyone shown why one species rather than another is better adapted for existence on account of the protective colors which it possesses. Ironically enough, it would appear that the animals getting along best in nature are those which are not "protected." This should not be considered as evidence against natural selection but only as a reminder that some things can be carried too far; modern genetics assumes natural selection to be true since a method by which a genetic population change could come about any other way is unknown. In regard to *Oeneis chryxus*, it can only be stated that an unbiased student must look into all factors of the environment and this has seldom been done by any observer of "protective coloration."

A search for predators of the adult *Oeneis chryxus* has not been successful. There is no known difference (that is, no visible difference observed) between the two races in the immature stages (larvae and pupae) and they are therefore irrelevant in this connection. The adults fly only during the warmer part of the day when there is sunlight; other times they are at hiding in the relative darkness which exists between rocks, among alpine plants and such places where color is of no value. Predators, therefore, in order to be selective, must prey upon the butterflies during that very limited time of day, and chiefly when they are in flight,[1] for only at that time is the color difference shown to its greatest advantage. Other insects and birds seem to be the only predators under these conditions. Grin-

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[1] One of Carrick's ('36) conclusions was that movement renders as void any protective resemblance present. However, the results of this paper should not be taken too seriously; there is great doubt as to the statistical significance of the experiments made. Movement has been mentioned by many naturalists as the basic factor rendering a concealed object conspicuous; its truth is much less difficult for a critical mind to imagine than some cases of "resemblances."

nell and Storer ('24) list only *Leucosticte tephrocotis dawsoni* Grin. (the Sierra Nevada Rosy Finch) and *Zonotrichia leucophrys leucophrys* (Forster) (Hudsonian white-crowned Sparrow) as whole or part time residents in the Arctic-alpine life-zone. These birds are seed eaters but occasionally capture insects. Observations have not shown them to eat *Oeneis* but these observations can only be classed as negative evidence, and not conclusive. No observations have shown other insects to eat *Oeneis* either, though further study will definitely be needed.

As stated above, there appear to be no general climatic differences between the various parts of the Arctic-alpine life-zone in the Sierra Nevada to which physiological differences between the color races of *Oeneis* might be attributed. However, microgeographic differences could exist, these being caused by different edaphic conditions, such as warmer microtemperature near the food plant due to a greater absorption of solar radiation by the dark-colored rocks. Developing larvae and pupae might be affected by the absorption of different wave-lengths of solar light (color), or by the absorption by the larvae of different chemical constituents from the food plant, which likewise might have been chemically different on account of the absorption from soil of different composition. These are factors which have received little attention from experimenters possibly because of the predatory-selection idea and cannot be verified at the present time. But as the color differences are almost certainly genetic, it cannot be assumed that the above effects change the color of the butterfly directly.[2] It may be that if a

given mutated gene or, more probably, a new combination of genes (which gives the brown or white color as a bi-product) gives the insect which possesses it greater suitability for living in the habitats where the above conditions prevail, it might have a greater chance for survival.

Perhaps it may be stated that eco-genotypical variation as illustrated by the species *Oeneis chryxus* is of more common occurrence among animals than is generally acknowledged. Since most of the published data of this sort have been among the vertebrate animals, the dogma of natural selection by predation (true though it may be in many instances) has overwhelmed any theory of ecological fitness. An account of the parallel between the genetic variation and ecological preferences is being prepared which may lead to an experimental verification of the parallel between the physiological conditions of the habitat and the genetics of color in animals.

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[2] The color differences are assumed to be most probably genetic because white populations exist and develop upon dark-rock areas where these areas are smaller than the effective breeding range of an individual butterfly. White individuals from the granitic region surrounding such an isolated dark-rock area could easily swamp and make ineffective any selective effect which might be operative.

## SUMMARY

The distribution of the color races of *Oeneis chryxus* in the Sierra Nevada is described. It is found that the races differ mainly in the color of the upper sur-

faces of the wings and that this coloration is found to be very closely correlated with the color of the habitats in which these races live. The question is raised as to the reason for this correlation and hypotheses are advanced and discussed to account for this "protective coloration," namely, selection by predators and selection by physiological fitness for the environment. The latter is thought by the author to be too severely neglected in cases of this sort and possibly to be the most probable hypothesis in this instance.

### APPENDIX

LOCALITIES FROM WHICH THE MATERIAL WAS COLLECTED

Collections made in June, July or August or sporadically since 1907. ("S" means "several.")[3]

| County | Locality | Elevation | Number |
|---|---|---|---|
| Nevada | Castle Peak Ridge | 8,500 | about 15 |
| " | Donner Summit | 8,000 | unknown |
| " | "Truckee" | — | — |
| Placer | Deer Park | 7,900 | 1 |
| " | Snow Mt. | — | 1 |
| " | Ward Peak | 8,800 | S |
| " | Ellis Peak | — | 4 |
| " " | — | S |
| El Dorado | Mt. Tallac | 9,000 | 30± |
| " " | Fallen Leaf Lake | — | S |
| " " | Pyramid Peak | 10,000 | — |
| " " | Echo Lake | 8,000 | S |
| — | "Lake Tahoe" | — | many |
| Amador | Silver Lake | 8,000 | 3 |
| Alpine | Freel's Peak | — | S |
| " | Ebbet Pass | 9,500 | 11 |
| " | Sonora Pass | 8,500 | 13 |
| " | " " | 10,000 | 2 |
| " | " " | 10,000 | 125+ |
| " | " " | 10,000 | 28 |
| Tuolumne | Slide Canyon | 10,500 | 1 |
| " | " " | 10,500 | 1 |
| " | North Peak, Conness | — | 10± |
| " | Young Lakes | — | 4 |
| " | Gaylor Lakes | 11,000 | 15 |
| " | Tioga Pass R. Sta. | 10,000 | 3 |
| " | " Lake | 10,000 | 6 |
| " | " Peaks | 11,000 | 34 |
| " | Mt. Dana | 11,000 | 4 |
| " | " Gibbs | 10,000 | 1 |
| " | " Dana | — | — |
| " | Mammoth Peak | 10,000 | S |

[3] Most of this material was personally checked by the author; a small part of it was not and error could have come in in this part. However, all the more important localities were either collected in or the material was checked by the author.

### APPENDIX—*Continued*

| County | Locality | Elevation | Number |
|---|---|---|---|
| Mariposa | Cathedral Lake | 10,000? | — |
| " | Florence " | 11,000? | — |
| " | Mt. Lyell | 12,000? | — |
| Mono | Virginia Lakes | — | S |
| " | Minaret Summit | 9,000 | 9 |
| " | Mammoth Pass | 9,000 | 1 |
| " | " Crest | 10,000? | 2 |
| " | "Mammoth" | — | many |
| " | Red Mt. | 11,000? | 4 |
| " | " " | 11,000? | 10 |
| " | " " | 11,000? | 10 |
| " | Panorama Dome | — | 4 |
| " | Red Lake | — | 2 |
| " | Barney Lake | — | 1 |
| " | Duck Summit | — | — |
| " | " Lake | — | 16 |
| " | Skeleton Lake | — | 1 |
| " | Rock Creek | 11,000 | 1 |
| Fresno | Huntington Lake | — | 1 |
| " | " " | | |
| " | Kaiser Crest | 10,000 | 140 |
| " | Mt. Hutching's Ridge | 10,450 | 1 |
| " | Bubbs Creek | 10,500 | 1 |
| Inyo | Bishop " | — | — |
| Tulare | Mineral King | — | 1 |

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# THE EFFECT OF OVERGRAZING AND EROSION UPON THE BIOTA OF THE MIXED-GRASS PRAIRIE OF OKLAHOMA [1]

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## INTRODUCTION

Overgrazing of pasturelands is one of the major problems facing the Oklahoma farmer today. Aside from soil erosion on cultivated land, excessive pasturing of prairie and woodland is perhaps our greatest agricultural menace. Greater runoff from grazing land as the vegetation is destroyed added to water lost from tilled soil has increased the flood problem not only in Oklahoma but throughout the country. Every effort has been made to put all tillable soil into cultivation and utilize only rough, wooded or rocky areas as pasture for all livestock maintained on the farm. If such land is lacking then a comparatively small amount of grassland is set aside for grazing of livestock.

Most people fail to realize that in order to maintain the best type of vegetation on grazing lands it is necessary to allow the plants to have a growth period in the spring during which reserves utilized in the production of new above-ground portions can be replaced or to reduce the number of animals pastured to the point where it is impossible for them to destroy all the new growth in the spring. The latter course is comparatively inefficient as many more animals could graze an area in the summer and fall if the vegetation is allowed to get a start in the spring. Early and continuous grazing soon eliminates the desirable or palatable species from the vegetation and their place is taken by unpalatable or inedible forms.

If overgrazing has been intense or of long duration, erosion may have completely removed much of the topsoil before it could be stabilized by inedible plants. In such cases a type of vegetation is to be found which is different from

that found on areas where overgrazing is less intense or of shorter duration.

The changes in fauna as overgrazing and erosion occur are not as easily determined as changes in flora. Insects must be studied over a period of at least a year and an adequate census of other animals taken. It is the purpose of this study to trace the biotic changes occurring under various degrees of overgrazing.

*Acknowledgments.*—The writer wishes to acknowledge the assistance given by various individuals during the course of this study. Gerald Acker aided with the field work and with the identification of the Orthoptera. Dr. A. I. Ortenburger cooperated in obtaining the identification of the mammals and Dr. Milton Hopkins with the work on plants. Thanks are due also to Dr. Melville Hatch of the University of Washington for identifying certain Coleoptera. Dr. A. O. Weese has aided the writer throughout the work by his suggestions and advice. To all others who have contributed in various ways I also extend my thanks.

## RELATED STUDIES

Several studies dealing with effects of overgrazing upon biotic communities have been made by workers at the University of Oklahoma. Coyner ('38) studied insect distribution and seasonal succession in overgrazed and normal grasslands over a period of a year (September 1, 1936 to September 1, 1937) in Oklahoma County. He found that Homoptera, Orthoptera, and Lepidoptera showed a definite preference for an overgrazed habitat while other orders showed a less definite distribution. It is well to know the changes in numbers of insects following overgrazing but more important to know the changes in species. For this reason this study endeavors to show the effect of overgrazing upon the

various species. Distribution of rodents in relation to overgrazed and normal grasslands in central Oklahoma was studied by Phillips ('35) who found that jackrabbits and deer mice prefer overgrazed areas while cottontail rabbits, ground squirrels and pocket gophers prefer normal grasslands. The results of the writer do not agree with Phillips in regard to the deer mice, the data of the author showing these mice to be most abundant in normal or slightly grazed grassland decreasing in abundance with increasing overgrazing but becoming very abundant when erosion occurs following very severe and prolonged overgrazing. Weese ('39) carried out an intensive study of the effect of overgrazing on insect populations in the Wichita Mountains Wildlife Refuge in Comanche County, Oklahoma for a period of thirty days and found that there was a striking qualitative and quantitative difference in insect populations on overgrazed and normal grassland. The total population of insects in overgrazed grassland was about four times as large as in normal grassland. He also found that the species which were numerous in ungrazed prairie were in most cases not the same ones which were abundant in overgrazed areas.

Overgrazed pastures on various types of soil in central Oklahoma were studied by Bruner ('26) who found the following: pastures on clay soils when continuously overgrazed showed more of the soil occupied by the short grasses and fewer tall grasses. When grazing was heavy and where it had been long continued almost all the tall grasses had been killed out. In pastures of this condition weeds are usually conspicuous. Of these, *Amphiachyris dracunculoides* (broomweed) is the most important. The most severely overgrazed pastures on clay soil showed the short perennial grasses being rapidly exterminated and a weedy flora having very little forage value taking their place. Vegetation on such pastures was found by Bruner to consist of *Amphiachyris dracunculoides, Hordeum pusillum, Achil-*

*lea lanulosa, Vernonia missourica, Dichrophyllum marginatum, Chloris verticillata* and *Schedonnardus paniculatus.* Most of the grasses of the climax prairie are gone.

Bruner did not consider erosion as a factor in his study. In this research stations were selected which resemble those described by Bruner and also some where the surface soil was eroded away following severe overgrazing. As far as vegetation on severely overgrazed pastures is concerned, the writer agrees with Bruner but is able to add more species to the list because of the more widespread nature of the study. Bruner (p. 38) summarized the effects of overgrazing as follows: "Early spring growth as well as the time of flowering and fruiting are retarded, grasses do not develop sufficiently to cover the soil and weedy plants are able to get a start, disturbance in the plant cover results in several important changes in the habitat, little humus is returned to the soil and its fertility is not maintained, lack of humus increases the runoff since decaying plant remains absorb large quantities of water, finally, the lack of a good plant cover promotes erosion of the steeper slopes."

In this study, flora and fauna of undisturbed native prairie are considered as the starting point and various degrees of grazing of this prairie are recognized. For this reason it is important to thoroughly analyze the biota of undisturbed prairie in order to understand changes which occur following overgrazing. For a thorough review of the literature dealing with the prairie biome see Carpenter ('40). Of the many studies on prairies of other regions only a few need be mentioned.

Hayes ('27) studied prairie insects of Riley County, Kansas. He found Hemiptera to be the most prominent order with *Lygus pratensis* the dominant species. Hymenoptera, on the other hand, were comparatively few in number, especially bees and wasps, notwithstanding the abundance of flowers.

The behavior of various species of plants under influence of grazing and erosion is more easily understood if the root relations are known. The work of Weaver ('24) on distribution of native plants in the Great Plains is outstanding.

As indicators of severe overgrazing in grasslands, Clements ('28) listed *Gutierrezia sarothrae, Aristida purpurea, Artemisia frigida, Grindelia, Opuntia, Psoralea, Petalostemon, Verbena, Vernonia, Euphorbia, Carduus, Solidago*, etc. Unbalance between various societies of the grassland indicates varying degrees of overgrazing. As the more palatable species are grazed, less palatable species increase because of the removal of competition. Under further grazing pressure, even the less palatable species are eaten until only spiny, poisonous or completely unpalatable species are left as permanent occupants, with short lived annuals coming in during various seasons. By now erosion has begun to take its toll of top soil and when this is gone it takes more than a short rest to restore the native species.

Recovery of overgrazed grasslands of Arizona with complete protection was studied by Griffiths (Clements, '28) who found that the grasslands appeared to regain their original productivity with approximately three years of complete protection. He also found evidence to show that ranges would improve if only lightly stocked, although improvement was much more rapid with complete protection. Sampson ('23) recommended light grazing following maturity of the seed in order to trample it into the ground.

## AREAS STUDIED

A number of areas were selected in early spring of 1938 on which to study the biota under conditions of no grazing, proper grazing, moderate overgrazing but no extensive erosion, severe overgrazing and some erosion and of severe overgrazing and erosion. At least two representatives of each stage were studied excepting in case of undisturbed prairie in

which nine areas were studied most of the season but only two remained unmowed or unburned at the end of a year.

The areas are distributed over Cleveland, Logan, McClain, and Oklahoma counties. The stations or areas have been grouped into five stages as described below.

Stage I, normal prairie.
Stage II, properly grazed.
Stage III, somewhat overgrazed, not eroded.
Stage IV, heavily overgrazed, somewhat eroded.
Stage V, severely overgrazed and eroded.

The term "overgrazed" is variously used and often no distinction is made as to intensity or degree of the condition. An area which supports only enough animals to properly graze it under conditions of normal rainfall may be overgrazed in drought years. Prairies in central Oklahoma quickly assume a typical "overgrazed" appearance even when grazed by a comparatively small number of animals if this grazing is carried on throughout the year. On the other hand a rather large number of animals on the same area would do little damage if the vegetation is allowed to get a start in spring before grazing starts. Thus far there is no way to determine the maximum number of animals an area can or should support because of the fact that weather during the grazing season will be the deciding factor when the maximum number of animals is present. The safest policy would seem to be to stock an area with the number of animals which can safely graze the area under subnormal conditions.

## METHODS

Visits were made every two weeks to the stations excepting during November, December, and January in which months only one visit was made per month. Insects were collected at each visit with 50 sweeps of a 14 inch net having a handle 4 feet long. The collections were killed in a cyanide jar and then wrapped in

paper toweling and later sorted and dried. Several specimens of each species were mounted for identification. In most cases this was done by comparison with checked specimens in the entomological collection at the University of Oklahoma. Dr. Melville Hatch of the University of Washington identified certain of the Coleoptera. Orthoptera were sent to Morgan Hebard of the Academy of Natural Sciences of Philadelphia for determination. Small mammals were trapped in October and fecal pellet counts of rabbits were made at this time. Skins were made of all mammals collected. Those of mice were identified by H. H. T. Jackson of the U. S. Biological survey. All specimens have been placed in the Museum of Zoology, University of Oklahoma. The only birds collected were meadowlarks. These were taken by a fellow worker, Mr. Thomas Baskett, who studied the distribution of meadowlarks in Oklahoma.

Plants were collected at blooming and pressed immediately. They were later identified by the writer. The grasses were checked by Mrs. Agnes Chase of the National Herbarium. All specimens of plants were placed in the Herbarium, University of Oklahoma. The relative abundance of the plants and total density of vegetation on each area were estimated at intervals.

Samples of soils were collected in July, using a hollow cylinder sampler one and one half inches in diameter. They were taken to a depth of six inches. Mechanical analyses by the hydrometer method as outlined by Bouyoucos ('36) were run on all samples. A determination of loss on ignition was made on each sample after drying at 105° C. for 48 hours then at 240° C. for one hour.

## CHANGES IN FLORA

*Data.*—In table I are listed the more important species of plants concerned in this study and their relative abundance under the different grazing conditions shown.

The dominants of the mixed grass

TABLE I. *Relative abundance of species of plants under various grazing conditions*

| Species | I | II | III | IV | V |
|---|---|---|---|---|---|
| Andropogon scoparius | 5 | 4 | 2 | 1 | |
| Andropogon furcatus | 1 | 1 | | | |
| Sorghastrum nutans | 1 | 1 | | | |
| Bouteloua curtipendula | 4 | 4 | 2 | 2 | 1 |
| Bouteloua gracilis | 2 | 2 | 2 | 1 | 1 |
| Bouteloua hirsuta | 2 | 3 | 4 | 2 | 1 |
| Buchloe dactyloides | 2 | 3 | 5 | 3 | 2 |
| Panicum scribnerianum | 2 | 1 | | | |
| Leptoloma cognatum | 2 | 1 | | | |
| Astragalus caryocarpus | 1 | | | | |
| Psoralea floribunda | 1 | 1 | 1 | | |
| Psoralea tenuiflora | 1 | 2 | 1 | 1 | |
| Petalostemon spp. | 1 | 1 | 2 | | |
| Pentstemon cobea | 1 | 1 | 1 | 2 | 1 |
| Liatris squarrosa | 1 | 1 | 1 | | |
| Solidago missouriensis | 1 | 1 | | | |
| Baptisia bracteata | 1 | 1 | 2 | | |
| Euphorbia corrolata | 2 | 1 | | | |
| Erigeron ramosus | 2 | 2 | | | |
| Oenothera serrulata | 1 | 1 | | | |
| Specularia biflora | 1 | 1 | | | |
| Sporobolus asper | 1 | 1 | | | |
| Hymenopappus carolinensis | 1 | 1 | 1 | 1 | 1 |
| Sabatia campestris | 1 | 1 | 1 | 1 | |
| Festuca octaflora | 1 | 2 | 1 | | |
| Nothoscordum bivalve | 1 | 2 | 2 | 1 | |
| Achillea millefolium | 1 | 2 | 1 | | |
| Anemone caroliniana | 1 | 2 | 2 | | |
| Vernonia missourica | | 1 | 1 | | |
| Oxalis stricta | 1 | 2 | 2 | 1 | 1 |
| Plantago purshii | 1 | 2 | 4 | 3 | 1 |
| Asclepidora spp. | 1 | 2 | 3 | 2 | 1 |
| Opuntia sp. | | | 1 | 2 | |
| Monarda citriodora | | 1 | 2 | 2 | 1 |
| Draba cunefolia | | 1 | 2 | 2 | |
| Paspalum pubescens | | 1 | 2 | 1 | |
| Schrankia spp. | | 1 | 1 | 1 | 1 |
| Thelasperma trifidum | | 1 | 2 | 2 | 3 |
| Amphiachyris dracunculoides | | 1 | 3 | 4 | 3 |
| Andropogon saccharoides | | | 1 | 2 | 2 |
| Chloris verticillata | | | 2 | 2 | 1 |
| Schedonnardus paniculatus | | | 1 | 2 | 1 |
| Sporobolus cryptandrus | | | 1 | 1 | |
| Euphorbia marginata | | | 1 | 2 | 2 |
| Daucus pusillus | | | 1 | 1 | |
| Lomatium daucifolium | | | 1 | 1 | 1 |
| Valerinella stenocarpa | | | 1 | 2 | 1 |
| Liatris punctata | | | 1 | 2 | 3 |
| Aristida purpurea | | | | 1 | 2 |
| Aristida longiseta | | | | | 2 |
| Aristida oligantha | | | 1 | 1 | 1 |
| Triodia pilosa | | | | | 3 |
| Echinacea angustifolia | | | 1 | 1 | 2 |

I—normal prairie, II—properly grazed prairie, III—overgrazed but uneroded prairie, IV—overgrazed and somewhat eroded and V—overgrazed and severely eroded.

prairie in central Oklahoma, *Andropogon scoparius* and *Bouteloua curtipendula*, show a decrease in abundance even under moderate grazing and are forced out of

the community when grazing is severe and prolonged. *Bouteloua curtipendula* persists somewhat longer than does *Andropogon scoparius*. As these grasses are eliminated from the vegetation, dominance is assumed by *Buchloe dactyloides, Bouteloua hirsuta* and *B. gracilis,* grasses usually subdominant in the climax mixedgrass prairie of this region but dominant in the western half of this prairie and in the short grass plains. Continued severe overgrazing accompanied by erosion produces conditions unfavorable to buffalo and gramma grass and they are replaced by a number of grasses, including *Chloris verticillata, Schedonnardus paniculatus, S. texanus, Festuca octaflora, Triodia pilosa, Hordeum pusillum, Aristida purpurea* and *A. longiseta* var. *robusta.*

Other changes in the composition of the vegetation also occur. Some species which are present in the original prairie flora in small numbers are soon eliminated by grazing. Certain of the larger legumes seem to be more or less unpalatable and may persist under conditions of considerable overgrazing. *Baptisia bracteata* is an excellent example of this group. *Baptisia australis* and *Petalostemon* spp., may persist for some time but are killed out before *Baptisia bracteata.*

*Discussion.*—Most perennial plants must complete their annual vegetative growth before fruiting. Early and heavy grazing does not allow replenishment of food reserves used in the early growth of the plants and starvation results. Annuals which flower and fruit quickly and without too great a display of foliage are frequently the only plants which can survive under conditions of severe overgrazing. Small perennials such as various wild onions (*Allium* spp.), crow poison (*Nothoscordum bivalve*), anemones, carrot-leaved parsley (*Lomatium daucifolium*) and others are able to grow and reproduce because they are not sought after by grazing animals. Species of plants found on the prairie are forced out in the order of their palatability or edibility. When erosion occurs following severe overgrazing, unpalatable or inedible species may drop out of the prairie community.

The plants which invade pastures as components of the original prairie vegetation and are killed are those which cannot compete with the original plants and which in various ways escape being eaten by domestic animals. *Amphiachyris dracunculoides, Vernonia missourica, Euphorbia marginata, Solanum rostratum, Bromus* spp., *Chloris verticillata, Schedonnardus paniculatus* and *Paspalum pubescens* are some common invaders.

In tables II and III is summarized the behavior of most of the species shown in table I. Plants which may be favored

TABLE II. *Behavior of species of plants under conditions of moderate grazing*

| Species forced out or greatly decreased in abundance | Species increasing more or less | Species invading | Species more or less unaffected |
|---|---|---|---|
| *Andropogon scoparius* *Andropogon furcatus* *Sorghastrum nutans* *Astragalus caryocarpus* *Erigeron ramosus* *Panicum scribnerianum* *Solidago missouriensis* *Specularia* spp. | *Achillea millefolium* *Asclepidora decumbens* *Opuntia* sp. *Buchloe dactyloides* *Bouteloua hirsuta* *Bouteloua gracilis* *Andropogon saccharoides* *Plantago* spp. *Sabatia campestris* *Verbena stricta* *Festuca octaflora* *Nothoscordum bivalve* *Allium* spp. *Oxalis stricta* *Lomatium daucifolium* | *Amphiachyris* *dracunculoides* *Vernonia missourica* *Schedonnardus* *paniculatus* *Bromus* spp. *Hordeum pusillum* | *Baptisia bracteata* *Psoralea* spp. *Oenothera serrulata* *Petalostemon* spp. *Hymenopappus carolinensis* *Pentstemon* spp. *Anemone caroliniana* *Senecio plattensis* *Lithospermum angustifolium* *Bouteloua curtipendula* |

TABLE III. *Behavior of species of plants under conditions of overgrazing and erosion*

| Species decreasing in abundance | Species increasing in abundance | Invading species |
|---|---|---|
| Asclepedora decumbens | Opuntia spp. | Chloris verticillata |
| Buchloe dactyloides | Houstonia angustifolia | Euphorbia marginata |
| Bouteloua hirsuta | Monarda citriodora | Solanum rostratum |
| Andropogon saccharoides | Draba cunefolia | Valerinella stenocarpa |
| Plantago spp. | Liatris punctata | Actinea linearifolia |
| Festuca octaflora | Echinacea angustifolia | Triodia pilosa |
| Nothoscordum bivalve | | Aristida purpurea |
| Allium spp. | | Aristida longiseta |
| Oxalis stricta | | Aristida oligantha |
| Amphiachyris dracunculoides | | Verbena bipinnatifida |
| Vernonia missourica | | Thelasperma trifida |
| Schedonnardus paniculatus | | |
| Bromus spp. | | |
| Hordeum pusillum | | |
| Baptisia bracteata | | |
| Psorales spp... | | |
| Pentstemon cobea | | |
| Anemone caroliniana | | |
| Bouteloua curtipendula | | |

by overgrazing alone are unable to tolerate conditions produced by erosion and as a consequence we find plants increasing or invading overgrazed areas then dropping out as erosion sets in.

## CHANGES IN FAUNA

*Numerical Data.*—Arthropods—General.

A comparison of the populations of insects and spiders is presented in table IV.

TABLE IV. *Number of specimens of each order taken under various conditions of grazing*

| Stage | I | II | III | IV | V |
|---|---|---|---|---|---|
| Coleoptera | 769 | 709 | 506 | 371 | 296 |
| Hemiptera | 315 | 214 | 416 | 687 | 263 |
| Homoptera | 598 | 690 | 620 | 750 | 224 |
| Hymenoptera | 63 | 78 | 44 | 219 | 332 |
| Diptera | 212 | 252 | 256 | 342 | 66 |
| Orthoptera | 841 | 863 | 1888 | 1116 | 827 |
| Lepidoptera | 46 | 58 | 96 | 72 | 164 |
| Arachnida | 634 | 540 | 654 | 530 | 220 |
| Total | 3473 | 3404 | 4480 | 4276 | 2392  18025 |

The number of species contributing to the totals for the orders shown in table IV are shown in table V. Only the identified species have been included.

*Coleoptera.*—The Coleoptera was one of the best represented orders of insects in undisturbed prairie but under conditions of overgrazing, the number of

TABLE V. *Total number of species in each order under various grazing conditions*

| | I | II | III | IV | V | Total |
|---|---|---|---|---|---|---|
| Coleoptera | 43 | 42 | 36 | 26 | 25 | 67 |
| Hemiptera | 25 | 23 | 23 | 29 | 18 | 44 |
| Homoptera | 17 | 13 | 17 | 17 | 20 | 23 |
| Hymenoptera | 9 | 9 | 8 | 7 | 6 | 14 |
| Diptera | 23 | 19 | 20 | 22 | 9 | 39 |
| Orthoptera | 19 | 22 | 25 | 24 | 21 | 30 |
| Total | 136 | 128 | 129 | 125 | 99 | 217 |

species and specimens was considerably reduced.

Table VII shows the changes in the number of species and specimens of beetles as various degrees of overgrazing occur.

The number of leaf beetles were found to be much less under conditions produced by overgrazing and erosion. Most of the species of Chrysomelidae listed in table VI do not survive in areas severely overgrazed and eroded. Meloidae show an increase in abundance as overgrazing increases while a great many other coleopterans seem to be favored by moderate grazing of the prairie.

*Hemiptera.*—Unlike most of the Coleoptera, Hemiptera in general seem to be favored by the changes produced by overgrazing. Most of the species decline in abundance or entirely drop out of a com-

TABLE VI. *Numerical distribution of species of Coleoptera under conditions of I—undisturbed prairie, II—properly grazed prairie, III—overgrazed prairie, IV—overgrazed and somewhat eroded prairie and V—overgrazed and severely eroded prairie*

| Families | Species | I | II | III | IV | V |
|---|---|---|---|---|---|---|
| Alticidae | Phyllotreta lewisii | 4 | 2 | 4 | 30 | |
| | Chaetocnema denticulata | 8 | | 16 | 2 | 2 |
| | Altica foliacea | 56 | 28 | 12 | 14 | 18 |
| | Oedionychis gibbitarsa | 1 | | 4 | | 2 |
| | Pleurostichus convexicaulis | 32 | 16 | 6 | 28 | |
| | Systena hudsonius | 88 | 150 | 20 | | |
| Chrysomelidae | Diabrotica 12-punctata | 8 | 6 | 2 | 2 | |
| | Diabrotica vittata | 6 | | | | |
| | Diabrotica atripennis | 40 | 2 | 26 | 10 | |
| | Galerucella notulata | | 22 | 22 | | |
| | Graphops varians | 6 | 2 | | 2 | |
| | Luperodes varicornis | 20 | 6 | 4 | | |
| | Nodonota clypealis | 36 | 2 | | | |
| | Pachybrachys morosus | 56 | 50 | 6 | 6 | |
| | Pachybrachys autolycus | 150 | 96 | 150 | 64 | 8 |
| | Saxinis omogera | | 4 | 4 | 2 | |
| | Typophorus canellus | 32 | 40 | 16 | | |
| | Zygogramma disrupta | | 14 | 50 | | |
| Carabidae | Discoderus parallelus | | 2 | 2 | | |
| | Lebia viridis | 4 | 2 | | | |
| Cerambycidae | Tetraopes collaris | | | 2 | 2 | |
| | Typocerus sinuatus | 8 | 60 | | 10 | |
| Coccinellidae | Hippodamia convergens | 4 | 10 | 6 | 2 | 2 |
| Curculionidae | Anthonomus nigrinus | 10 | | | | 4 |
| | Cetrinus modestus | 1 | 4 | 2 | 2 | |
| | Hormops aducens | 6 | | 1 | | |
| | Tanymecus lacaena | 16 | 22 | 2 | 2 | 2 |
| | Mylostylus tenuis | 36 | 120 | 16 | 12 | 2 |
| | Miscellaneous species | 14 | 34 | 8 | 14 | |
| Dermestidae | Cryptorhopalum picicorne | 12 | 20 | 8 | 6 | |
| Melyridae | Collops quadrimaculatus | 28 | 56 | 34 | 56 | 58 |
| Meloidae | Epicauta maculata | 8 | 8 | 20 | 8 | 10 |
| | Epicauta trichrus | | | | | 6 |
| | Epicauta ferruginea | 4 | | 2 | 24 | 22 |
| | Macrobasis unicolor | | 4 | 12 | | |
| | Macrobasis immaculata | | | | | 4 |
| Mordellidae | Mordella melaena | 20 | 32 | 10 | 16 | 8 |
| Phalacridae | Phalacrus simplex | 8 | 2 | 6 | 16 | |
| | Phalacrus politus | | | 15 | | |

munity after the soil has eroded to a point where the density of the vegetation is greatly reduced and the composition changed. The changes in total number

of species and specimens of true bugs under conditions of proper and overgrazing are shown in table VIII.

In table IX are listed the more impor-

TABLE VII. *Table showing the changes in the numbers of species and specimens of Coleoptera as overgrazing occurs*

| Stage | I | II | III | IV | V | Total |
|---|---|---|---|---|---|---|
| Species | 43 | 42 | 36 | 26 | 25 | 67 |
| Specimens | 769 | 709 | 506 | 371 | 296 | 2651 |

TABLE VIII. *A comparison of the species and specimens of true bugs under various grazing conditions*

| Stage | I | II | III | IV | V | Total |
|---|---|---|---|---|---|---|
| Species | 25 | 23 | 23 | 29 | 18 | 44 |
| Specimens | 315 | 214 | 416 | 687 | 263 | 1895 |

TABLE IX. *Numerical distribution of the more important species of Hemiptera in the prairie following various degrees of overgrazing and erosion.   (See explanation in title of Table VI.)*

| Family | Species | I | II | III | IV | V |
|---|---|---|---|---|---|---|
| Miridae | Adelphocoris rapidus | 25 | 2 | 2 | 2 | |
| | Lygus pratensis | 6 | 42 | 10 | 58 | |
| | Platytylellus circumcinctus | 2 | | | 4 | 2 |
| | Polymerus basalis | 28 | 2 | 34 | 100 | 22 |
| | Strongylocornis stygicus | | 20 | | | 4 |
| Pentatomidae | Thyanta custator | 2 | 8 | 12 | 24 | 8 |
| | Mecidia longula | 24 | 50 | 42 | 20 | 6 |
| | Peribalus abbreviatus | 4 | | 8 | 18 | |
| | Peribalus limbolarius | | 12 | 50 | 2 | |
| | Prionosoma podoploides | 2 | 2 | 8 | 30 | |
| | Trichopepla semivittata | 12 | 10 | 56 | 38 | |
| Lygaeidae | Lygaeus kalmii | | | | 58 | 50 |
| | Lygaeus reclivatus | 8 | 4 | 2 | 4 | 10 |
| | Ortholomus jamaicensis | 72 | 12 | 4 | 4 | 16 |
| | Ortholomus sp. 7 | 8 | 8 | 6 | 6 | 2 |
| Corimelaenidae | Corimelaena quadrisignata | 16 | 2 | 10 | 6 | 100 |
| | Galgupha nitiduloides | 60 | 10 | 100 | 80 | 6 |
| Coreidae | Chariesterus antennator | 2 | | 3 | 20 | |
| Corezidae | Harmostes reflexulus | 20 | 18 | 16 | 36 | 8 |

tant species of Hemiptera with the number of each taken under various grazing conditions.

*Homoptera.*—The Homoptera, like the Hemiptera, show an increase in abundance as the degree of overgrazing increases but the number of specimens is greatly reduced following severe erosion of the soil.   Table X shows these data.

Although the total number of speci-

TABLE X. *Changes in the number of species and specimens of Homoptera under various grazing conditions*

| Stage | I | II | III | IV | V | Totals |
|---|---|---|---|---|---|---|
| Species | 17 | 13 | 17 | 17 | 20 | 23 |
| Specimens | 598 | 690 | 620 | 750 | 224 | 2882 |

mens of homopterans was less under conditions of severe overgrazing, the number of species taken was greater than under

TABLE XI. *Numerical distribution of the more abundant species of Homoptera in the prairie following various degrees of overgrazing and erosion.   (See explanation in title of Table VI.)*

| Family | Species | I | II | III | IV | V |
|---|---|---|---|---|---|---|
| Cicadellidae | Chlorotettix unicolor | 138 | 178 | 66 | 30 | 8 |
| | Deltocephalus inimicus | 30 | 16 | 34 | 4 | 22 |
| | Deltocephalus sp. 14 | | | | 24 | 60 |
| | Deltocephalus sp. 15 | | | | 144 | 10 |
| | Driotura robusta | | 16 | | 2 | |
| | Empoasca viridescens | 36 | 46 | 200 | 18 | 20 |
| | Euscelis obscurinervis | 12 | 40 | 34 | 90 | 14 |
| | Helochara communis | | | 10 | 44 | 4 |
| | Helochara sp. 23 | | | 38 | 54 | 12 |
| | Mesanua nigridorsum | 12 | 84 | 160 | 30 | 2 |
| | Oncometopia lateralis | 10 | | 2 | 32 | 2 |
| | Xerophloea major | 18 | 2 | 2 | | 2 |
| | Xerophloea viridis | 2 | 20 | | | 6 |
| Membracidae | Campylenchia latipes | 45 | 128 | 42 | 220 | 10 |
| | Stictocephala festina | 40 | 12 | 12 | 12 | 4 |
| | Vanduzea arguta | 4 | 2 | 4 | 4 | 16 |
| Fulgoridae | Scolops spurcus | 4 | 54 | 28 | 38 | 6 |
| Cercopidae | Aphrophora quadrinotata | 200 | 92 | 4 | | 22 |

TABLE XII. *The species and specimens in each family of orthopterans taken under various grazing conditions*

| Stage | I | II | III | IV | V |
|---|---|---|---|---|---|
| | 13 | 16 | 20 | 20 | 18 |
| Acrididae | 579 | 580 | 1746 | 1044 | 707 |
| | 3 | 3 | 3 | 3 | 1 |
| Tettigonidae | 70 | 50 | 22 | 6 | 6 |
| | 1 | 1 | 1 | | 1 |
| Phasmatidae | 90 | 106 | 46 | | 2 |
| | 1 | 1 | | | |
| Mantidae | 2 | 3 | | | |
| | 1 | 1 | 1 | 1 | 1 |
| Gryllidae | 100 | 124 | 74 | 62 | 112 |

any other condition. In table XI are shown the distribution of the species of Homoptera.

*Orthoptera.*—The Orthoptera concerned in this study fall into five families. table XII shows the number of species and specimens in each family in each stage of grazing.

The Acrididae constitute by far the largest group of orthopterans found in the prairie and its complexes in central Oklahoma. The place in a food chain filled by grasshoppers is large and important. The distribution of the species of Orthoptera is shown in table XIII.

*Diptera.*—The Diptera were not well represented in the 1938 collections used in this study if the figures given by Coyner ('38) for the normal and overgrazed situations are compared with those obtained by the writer.

| | Normal prairie | Overgrazed prairie | Year |
|---|---|---|---|
| Coyner | 406 | 974 | 1936 |
| Smith | 190 | 342 | 1938 |

TABLE XIII. *Numerical distribution of the more important species of Orthoptera in prairies of various conditions. (See title of Table VI.)*

| Family | Species | I | II | III | IV | V |
|---|---|---|---|---|---|---|
| | Melanoplus confusus | 75 | 47 | 99 | 84 | 45 |
| | Syrbula admirabilis | 46 | 11 | 45 | 16 | 2 |
| | Mermiria maculipennis | 26 | 19 | 62 | 24 | 3 |
| | Arphia simplex | 14 | 12 | 6 | | 4 |
| | Acrolophitus hirtipes | 12 | 20 | 10 | | 20 |
| | Boopedon gracile | 2 | 8 | 16 | 18 | 2 |
| | Orphulella speciosa | 8 | 2 | 11 | 6 | 3 |
| | Melanoplus bivitattus | 10 | 36 | 100 | 9 | 14 |
| | Ageneotettix deorum deorum | 3 | 3 | 2 | 13 | |
| | Melanoplus packardii | 14 | 40 | 85 | 10 | 60 |
| Acrididae | Chorotophaga viridifasciata | ? | 4 | 10 | 10 | |
| | Hesperotettix s. speciosus | 4 | 2 | | | |
| | Schistocerca americana | 8 | 5 | | | |
| | Hespertettix viridis pratensis | 4 | 2 | | | |
| | Hippiscus rugosus | | 3 | 67 | 16 | 4 |
| | Hesperotettix v. viridis | | 7 | 18 | 27 | |
| | Melanoplus bispinosus | | 6 | 8 | 4 | 10 |
| | Pardalophora sausseri | | | 45 | 6 | 41 |
| | Brachystola magna magna | | | 2 | | 15 |
| | Hadrotettix trifasciatus | | | 25 | 37 | 57 |
| | Melanoplus regalis | | | 22 | | 11 |
| | Phlibostroma quadrimaculata | | | 34 | 10 | |
| | Sparagemon equale and S. collare | | | 11 | 15 | 22 |
| | Neoconocephala robusta crepitans | 6 | 4 | 4 | 2 | |
| Tettigoniidae | Conocephalus strictus | 18 | 28 | 16 | 2 | 6 |
| | Scudderia texana | 48 | 18 | 2 | 2 | |
| Phasmatidae | Diapheromera veili veili | 90 | 106 | 46 | | 2 |
| Gryllidae | Oecanthus nigricornis argentinus | 100 | 124 | 74 | 62 | 112 |
| Mantidae | Stagmomantis caroliniana | 2 | 3 | | | |

The Muscidae and Metopidae were by far the best represented families of the Diptera, both in species and specimens. Table XIV shows these data.

TABLE XIV. *The number of species and specimens of Diptera taken under different degrees of grazing*

| Families | I | II | III | IV | V | |
|---|---|---|---|---|---|---|
| Muscidae | 6 | 7 | 6 | 5 | 3 | species |
| | 95 | 130 | 118 | 146 | 38 | specimens |
| Metopidae | 9 | 8 | 10 | 9 | 3 | species |
| | 54 | 96 | 116 | 96 | 22 | specimens |
| Tabanidae | 2 | 0 | 2 | 3 | 1 | species |
| | 4 | 0 | 4 | 6 | 2 | specimens |
| Asilidae | 2 | 1 | 1 | 2 | 0 | species |
| | 6 | 14 | 2 | 30 | 0 | specimens |
| Syrphidae | 1 | 1 | 1 | 1 | 1 | species |
| | 10 | 16 | 6 | 52 | 2 | specimens |
| Trypaneidae | 2 | 1 | 2 | 1 | 1 | species |
| | 21 | 4 | 18 | 12 | 2 | specimens |
| Total species | 22 | 18 | 22 | 21 | 9 | |
| Total specimens | 190 | 260 | 264 | 342 | 66 | |

*Lepidoptera.*—This order of insects was poorly represented during this study. Identification of adults taken by the sweeping method of collection is very difficult and the naming of lepidopteran larvae is not practicable. For these reasons, the moths and butterflies, both as adults and larvae, are presented as the total number of specimens taken in each case rather than by the number of species.

TABLE XV. *The number of Lepidoptera taken under different degrees of grazing of the prairie*

| | I | II | III | IV | V |
|---|---|---|---|---|---|
| Number of specimens | 46 | 58 | 96 | 72 | 164 |

*Hymenoptera.*—The only members of this group to receive attention during this study were the flying forms. Ants and other ground forms were largely neglected. The Andrenidae are usually the most abundant hymenopterans in climax prairie in this region. These mining bees become very abundant as overgrazing and erosion bring about certain changes in the vegetation. Although a good many species were taken which were represented by only one or two specimens, the families listed in table XVI include the majority of species and specimens.

TABLE XVI. *Numerical distribution of Hymenoptera under various conditions of overgrazing and erosion*

| Family | I | II | III | IV | V |
|---|---|---|---|---|---|
| Andrenidae | 39 | 46 | 20 | 180 | 300 |
| Braconidae | 2 | 9 | 4 | 30 | 6 |
| Chalcididae | 8 | 6 | 4 | 10 | — |
| Ichneumonidae | 12 | 15 | 12 | 4 | — |

*Arachnida.*—Spiders occurred rather uniformly in all types of areas and did not show a marked decrease in abundance until most of the ground cover was gone and the insect population had changed considerably. The spiders were not sorted into species since in most cases those taken were juveniles. Table XVII presents the data concerning the distribution of the specimens of Arachnida.

TABLE XVII. *Total number of Arachnida taken under various conditions of grazing*

| Stage | I | II | III | IV | V |
|---|---|---|---|---|---|
| Number of specimens | 634 | 540 | 654 | 530 | 220 |

*Birds.*—The birds of the undisturbed prairie do not persist long under conditions produced by overgrazing. Overgrazed pastures are often used as feeding grounds by meadowlarks and other insect-eating birds. The increased population of grasshoppers in such areas probably accounts for this fact. Moderately grazed prairies were found to have a larger number of nesting meadowlarks than undisturbed prairie. Horned larks, dickcissels and song sparrows were not sufficiently numerous in any type of area to give comparative data.

*Mammals.*—Small mammals were trapped during October, using ordinary mouse traps. Twenty traps were used on each area for two successive nights. Table XVIII shows the actual catch of each species on each type of area.

TABLE XVIII. *The actual total catch of small mammals under different degrees of grazing*

|  | I | II | III | IV | V |
|---|---|---|---|---|---|
| Deer mice (*Peromyscus maniculatus bairdii*) | 4 | 5 | – | 3 | 8 |
| Harvest mice (*Reithrodontomys montanus griseus*) | 1 | 2 | 2 | – | – |
| Pocket mice (*Perognathus hispidus spilotus*) | – | 1 | 1 | 1 | 2 |
| House mice (*Mus musculus*) | 1 | – | – | – | – |
| Cotton rat (*Sigmodon hispidus texianus*) | 1 | – | – | – | – |
| Shrew (*Blarina brevicauda caroliana*) | ? | 2 | – | – | – |

Table XIX shows the pellet count for the rabbits and figures representing the relative abundance of the dens, runs and mounds of ground squirrels, moles and gophers respectively. Five indicates great abundance, one indicates rarity with the other numbers indicating intermediate degrees of abundance. Pellet abundance is expressed as the average number of pellets per square foot.

TABLE XIX. *Abundance of pellets, dens, runs and mounds of rabbits, ground squirrels, moles and gophers*

| Stage | I | II | III | IV | V |
|---|---|---|---|---|---|
| Cottontail (*Silvalagus floridanus alacer*) | .15 | .35 | .17 | .90 | 1.4 |
| Jackrabbit (*Lepus melanotus californicus*) | .15 | .25 | .36 | 1 | 1.4 |
| Ground squirrel (*Citellus tridecimlineatus*) | 1 | 2 | 2 | 2 | – |
| Mole (*Scalopus aquaticus*) | 2 | 2 | – | – | – |
| Gopher (*Geomys bursarius*) | 2 | 3 | 1 | – | – |

CHANGES IN SOILS

The soil samples were collected as described previously. The soil was air dried and mechanically analyzed following the procedure outlined by Bouyoucos ('36). Ignition tests after drying 48 hours at 105° C. were made. Data obtained are presented in table XX.

TABLE XX. *Results of soil analyses in percentages*

| Constituent | I | II | III | IV | V |
|---|---|---|---|---|---|
| Clay | 24 | 22 | 27 | 29 | 30 |
| Silt | 24.5 | 31 | 32 | 17 | 26 |
| Sand | 48.4 | 44 | 38.5 | 51.5 | 42 |
| Organic matter | 3.61 | 3 | 2.65 | 2.5 | 2.3 |

It is not the purpose of this paper to go into changes in soils following overgrazing and erosion and data on soils are presented merely to show certain trends. The distinction between sand and silt seems to be more a matter of size of particles rather than a difference in physical and chemical properties. When the percentages of silt and sand are added, we get a series of figures showing a gradual decline in percentage of coarser particles in soil as overgrazing and erosion proceed. On the other hand, the percent of clay in the upper six inches of soil shows a continuous increase as erosion becomes severe. The amount of organic matter in soil declines steadily as overgrazing continues and has been reduced to 34 per cent below that of undisturbed prairie in areas both overgrazed and eroded. The figures on soils indicate that recovery will not always be merely a matter of the original plants coming back into the vegetation when grazing is stopped but will be a process of succession because certain changes must be made in the soil before prairie plants can again occupy it.

CHANGES IN FAUNA: DISCUSSION

*Arthropods—General.*—Although the total number of insects increases under conditions of overgrazing, the total number of species shows a decline. The Orthoptera is the only group of insects to show an increase in both total number of species and total number of specimens when prairie is overgrazed. The Homoptera is the only order found to have more species under conditions of severe overgrazing and erosion. When erosion oc-

curs during long continued overgrazing, radical changes in the habitat are produced. The prairie vegetation is almost completely replaced by a few species which are tolerant of eroded soil. Insects associated with climax vegetation almost all drop out under conditions produced by erosion. Certain species which invade overgrazed areas may increase in abundance under conditions of severe erosion. The behavior of the various species will be discussed as each order is taken up.

*Coleoptera.*—The Coleoptera show more effect from overgrazing and erosion than do most of the other orders of insects. The Chrysomelidae in particular show a remarkable drop in species and specimens under such conditions. The native prairie yielded 9 species and 354 specimens while severely eroded pastures showed only one species of leaf beetle and eight specimens. Overgrazing alone seemed more favorable for the chrysomelids than overgrazing plus erosion since 9 species and 260 specimens were taken from overgrazed pastures. Three species of leaf beetles were taken from overgrazed pastures and not from prairie. These included *Galerucella notulata, Saxinis omogera* and *Zygogramma disrupta.* In another study the writer found these forms to be associated largely with midseral and sub-climax communities.

Table VI shows the behavior of members of the various families of Coleoptera under grazing conditions. It will be noted that the Meloidae is the only family which shows an actual increase in species and specimens in eroded pastures. The blister beetles have a rather complicated life history. The eggs of certain species are laid near pods of grasshopper eggs. The larvae feed on the grasshopper eggs. The larvae of other species complete their development in the nests of bees. Grasshoppers and mining bees are both abundant in overgrazed and eroded pastures.

*Hemiptera.*—The true bugs tolerate changes in the habitat produced by overgrazing better than do Coleoptera. Of the 24 species listed in table VII, ten show a definite increase in abundance under conditions of overgrazing. Five species of hemipterans were taken from pastured areas but not in undisturbed prairie. These included *Strongylocornis stygicus, Peribalus limbolarius, Solubea pugnax, Lygaeus kalmii* and *Blissus leucopterus.* In drought years these species probably would be found in the prairie. The spring of 1938, the year this study was carried out, was exceptionally wet and this may account for the small numbers of all insects being taken.

When erosion accompanies overgrazing, a marked effect is noted on the number of species and specimens of true bugs to be taken. Changes in the composition of the vegetation doubtless causes many phytophagous hemipterans to drop out of a community.

Continued production of new shoots by perennial grasses when they are grazed may to a certain extent provide better feeding conditions than are to be found in undisturbed prairie.

*Homoptera.*—Leaf hoppers showed a marked increase in the number of specimens to be taken when the prairie was overgrazed. The number of species increased when erosion accompanied overgrazing although the number of specimens per species showed a marked drop. As with Hemiptera, constant production of tender shoots following grazing of the vegetation probably provides an ideal source of food for leaf hoppers. Table XI shows the behavior of the various species of Homoptera under different conditions of grazing.

*Orthoptera.*—From the standpoint of total numbers present and size of individuals, members of the Orthoptera constitute one of the most important groups of insects of grazing lands. Previous studies by Weese ('39) and Coyner ('38) showed that there is a constant difference between the number of grasshoppers in ungrazed and grazed native prairie, the latter always having the larger population of these insects.

Data obtained during this study have confirmed the observations of these writers and showed that there is also an increase in the number of species of orthopterans when prairie is grazed. Overgrazing of mixed grass prairie causes an increase in the area occupied by short grasses such as *Buchloe dactyloides* and *Bouteloua hirsuta* and thereby produces a type of vegetation similar to that found further west.

Certain species of grasshoppers were taken only in pastures having almost pure stands of short grasses. *Phlibostroma quadrimaculata, Melanoplus regalis,* and *Brachystola magna* were taken only in such areas. When considerable soil surface is exposed as in the case of severe overgrazing and erosion, *Hadrotettix trifasciatus* becomes very abundant. Other species common in undisturbed prairie were found to be much more numerous in overgrazed pastures. Included in this group are *Melanoplus packardii, M. bivitattus, Mermiria maculipennis, Sparagemon collare* and *equale, Pardalophora* spp. and *Hippiscus rugosa.* Other species of Orthoptera listed in table XIII either were taken in too small numbers to indicate habitat preferences or were rather equally distributed in the various types of areas.

Orthoptera not only consume a great deal of vegetation which might otherwise be used by livestock but they supply in turn a great deal of food to animals feeding on insects. Overgrazed pastures do not provide a favorable habitat for most birds and small mammals which normally utilize grasshoppers as a portion of their food. This may be a factor contributing to the increase in abundance of these insects. Reduction in fungus disease among the grasshoppers might be expected since the short vegetation would allow rapid drying of the soil surface following rains. The greater amount of exposed soil surface is also an important factor favoring the breeding of most species of acridians.

*Diptera.*—The flies taken during the course of this study were chiefly those feeding on flesh or refuse. This is to be expected in collection from areas in which livestock feed. The total number of dipterans taken in the various stages of grazing shows an increase from the native prairie to areas extremely overgrazed and somewhat eroded. A great deal of erosion following overgrazing apparently is not favorable for reproduction of many species of flies.

*Hymenoptera.*—These insects play a rather complex role in a biotic community. Although in most cases few in number, their activities are varied. Leaf cutting, gall formation and pollen and nectar collection are important activities of Hymenoptera affecting plant life. Parasitism of hymenopterans upon each other and upon other animals is widespread and complex.

The climax prairie community yields the largest number of species although the number of specimens is usually less than in disturbed areas. Certain forms may become very abundant when habitat conditions become favorable for them. The mining bees (Andrenidae) furnish an excellent example. These bees are the most abundant species of hymenopteran in undisturbed prairie yet when perennial grasses give way to various forbs, the number of andrenids increases enormously. This increase is favored by two factors. These are (1) the more exposed nature of the soil surface in eroded areas and (2) the increased number of forbs may provide more pollen and nectar for these mining bees.

*Lepidoptera.*—The numerical distribution of Lepidoptera indicates that as the number of forbs in the vegetation increases, the number of lepidopterans also increases. The change in species making up the total number of these insects was not ascertained due to the tattered condition of the adults taken in routine sweeping and to the difficulty of identifying the larvae.

*Arachnida.*—The total number of spiders in each of the various stages of

grazing and overgrazing showed little variation until severe erosion is encountered. Under such conditions the populations of all insects showed a sharp decline and this may account for the reduction in the number of spiders in these stages since they feed on insects.

*Mammals.*—Mammals which have their dens and runs beneath the surface of the ground are often more tolerant of conditions produced by overgrazing than are those forms living wholly above ground. Food and cover must be present in minimum amounts for each species in order for them to survive.

The prairie deer mouse lives in burrows in the ground and emerges at night to feed. Seeds form the bulk of its diet although animal matter may be eaten at times. Cover does not seem to be a controlling factor since these mice are very abundant in open fields, abandoned areas and on rocky ground. They also are found throughout climax prairie but are not as abundant here as in disturbed or subclimax areas. Vegetation composed of plants producing large seeds provides an especially fine habitat for these animals. Data presented in table XV show that when the prairie is moderately grazed, the number of deer mice is greater than in undisturbed prairie and when the tall grasses and legumes are replaced by buffalo and gramma grass their number is less than in the original prairie. Areas which show much erosion were found to have the largest population of these mice. Following severe erosion, the soil is usually occupied by vegetation which contains an abundance of forbs which produce seeds sought by deer mice. *Thelasperma trifidum, Echinacea pallida* and *Liatris punctata* are among the more abundant forbs on eroded pastures in this area. Sometimes other plants such as *Helianthus* spp., *Aplopappus ciliatus, Euphorbia marginata* and *Solanum rostratum* may be scattered over eroded pastures.

The harvest mouse was taken only in areas having a fairly dense cover of vegetation. These mice were not taken in eroded areas nor were they common in climax prairie vegetation. Other studies by the writer have shown that the harvest mouse finds its optimum habitat conditions in central Oklahoma in sandy prairie areas such as are found along the major streams. The pocket mouse is found in the undisturbed prairie only around rocky or gravelly outcrops. When prairie is intensely grazed and erosion has removed much of the topsoil, these mice become comparatively abundant.

Cotton rats feed during the daytime, eating tender grass stems and seeds of any forbs which may be available. Insects and the remains of other animals are eaten by these rats during periods of food scarcity.

Sometimes these animals become so abundant that their numbers may reach plague proportions. Natural controls such as disease, food shortage, predators and other factors soon reduce their numbers to a point where they do not constitute a menace to the biotic community. These rats normally live in thickets, tall grass and underbrush and are not to be found far away from such cover.

Although the cottontail rabbit is found throughout the prairie, it is present in the greatest numbers in brush, weedy fields and rough ground. Overgrazing produces a type of vegetation favorable to the feeding activities of these animals but provides poor cover unless gullies, ravines or brushy areas are present or nearby. Fecal pellet counts indicate that rabbits come into overgrazed pastures at night to feed on the tender shoots which are produced following grazing of the vegetation. When many of the grasses are replaced by forbs following erosion, the total number of cottontail rabbits utilizing such areas as feeding grounds is greater than that found in undisturbed prairie. Food is probably obtained from other sources a part of the year because during winter not much food remains on eroded areas.

The jackrabbit is typically a plains animal and shows a marked increase in abun-

dance when grazing eliminates most of the taller grasses from mixed prairie vegetation. Vorhies and Taylor ('33) found that in Arizona, overgrazed areas where forbs were abundant had a larger population of jackrabbits than areas covered with climax grasses.

Table XXI shows the relative abundance of the various small mammals considered in this study. Abundance is indicated by a scale of 1 to 5. One indicates an infrequent or rare species while 5 indicates great abundance. This method is used to put all the data concerning mammals on a comparative basis.

TABLE XXI. *Relative abundance of small mammals*

| Name | I | II | III | IV | V |
|---|---|---|---|---|---|
| Deer mouse | 3 | 4 | 1 | 3 | 5 |
| Harvest mouse | 1 | 2 | 1 | 1 | – |
| Pocket mouse | – | 1 | 1 | 1 | 1 |
| House mouse | 1 | 1 | | | |
| Cotton rat | 2 | | | | |
| Shrew | 1 | 1 | | | |
| Cottontail | 2 | 3 | 3 | 3 | 4 |
| Jackrabbit · | 1 | 1 | 2 | 3 | 2 |
| Ground squirrel | 1 | 1 | 2 | 2 | |
| Mole | 1 | 1 | | | |
| Gopher | 1 | 2 | 1 | | |

The total number of species of small mammals is greatest in undisturbed prairie and least in overgrazed and eroded areas. The least abundance of all small mammals is reached in the severely overgrazed but uneroded areas and again increases when erosion begins and new plants invade the community. Animals favored by a sparse, weedy vegetation show their greatest abundance on the eroded areas. In this group are found deer mice, pocket mice and cottontail rabbits. Ground squirrels and jackrabbits are especially favored when the taller grasses are eliminated from the vegetation, leaving a dense mat of short grasses and clumps of forbs. When overgrazing kills out much of the short grass, broomweed becomes the dominant species of plant. Under such conditions the number of jackrabbits decreases.

## A Proposed Grazing Plan for Central Oklahoma

In order to allow removal of the maximum amount of vegetative material each year and at the same time maintain the prairie in its most productive condition, it will be necessary to practice deferred rotational grazing. On any given farm pasture area should be divided into three parts, only one of which is grazed in the spring during any given year, thus any one portion would be spring-grazed only every third year. Areas so grazed would not be used in the summer of that year. The other two portions would either both be grazed in summer and fall or one grazed and the other used for hayland. By this plan perennial plants would have two springs and one complete summer to recover for every spring grazing they receive. Summer and fall grazing has far less effect upon perennial vegetation than spring grazing so that the rest periods indicated will allow sufficient recovery to maintain the vegetation in its best condition.

The majority of the pastures of central Oklahoma are not as over-stocked as conditions would indicate but they are in most cases grazed year around and thus the perennial plants have been unable to maintain themselves. An outline of the above plan is shown in table XXII.

Before such a plan can be applied to a region such as central Oklahoma where the pasture land is nearly all badly depleted due to continuous grazing, it will be necessary to make some provision for allowing the vegetation at least partially to recover. Complete protection for at least three years will be necessary in most cases although many eroded areas will require a much longer time to recover.

### Summary and Conclusions

The work of Weaver and Fitzpatrick ('34) and others have shown that the removal of vegetative growth after maturity has little effect upon the future growth and reproduction of the components of

TABLE XXII.  *Schedule of deferred rotational grazing for pasture lands of central Oklahoma*

| Treatment | Area 1 | Area 2 | Area 3 |
|---|---|---|---|
| 1st year | Spring grazed. | Summer and fall grazed. | Summer and fall grazed or cut for hay. |
| 2nd year | Summer and fall grazed. | Spring grazed. | Summer and fall grazed or cut for hay. |
| 3rd year | Summer and fall grazed. | Summer and fall grazed or cut for hay. | Spring grazed. |
| 4th year | Spring grazed. | Summer and fall grazed. | Summer and fall grazed or cut for hay. |

the prairie. On the other hand, it has been the universal experience of cattlemen that when grasslands are grazed heavily and continuously throughout the year the original palatable components are replaced by inedible or unpalatable species. It has been the observation of the writer that when grazing is suspended during the spring months in central Oklahoma, later grazing has little more effect upon the composition of the vegetation than does mowing for hay in the summer.

Pasturing of perennial grasses in spring just as new stems and leaves are developing means more than just removing a portion of the plant. The young shoots have been produced at the expense of reserves in the underground parts of the plant and their premature removal does not allow the reserves to be replenished. Thus the vitality of the perennial plants is rapidly depleted. Removal of the same parts after they have attained their full size would allow them to return to the underground stems and roots a quantity of food equal to that utilized in their product and at the same time would provide far more food for the harvesting animal. The effects of overgrazing upon the biota of the prairie may be summarized as follows:

(1) Early and continuous overgrazing depletes the reserves of perennial plants thus eventually killing them. The area formerly occupied by the taller perennial plants may be occupied (a) by perennials or annuals less edible or palatable, or (b) ones which cannot be so completely grazed off such as the short grasses, or (c) if these are lacking then erosion may remove the rich topsoil thus preventing the original vegetation from returning before certain changes have been wrought by subclimax species.

(2) Light or seasonal grazing tends to favor the spread of certain species of plants, especially those least sought after by grazing animals and those favored by the grazing off of the taller forms.

(3) The effect of grazing upon the fauna of the grasslands is less obvious until studied. Light grazing seems to favor the majority of insects since a great many species showed an increase in such areas. Conditions produced by overgrazing cause the dropping out of many species but enables grasshoppers to increase enormously in abundance. The best control for these insects is to allow the vegetation to return to as near original conditions as possible yet get the optimum return from the vegetation each year.

(4) Habitat conditions in severely overgrazed areas appear to be very unfavorable to chrysomelids (leaf beetles) but favorable to the Meloidae (blister beetles). The Curculionidae are favored by light grazing but are much less abundant in severely overgrazed areas. Other groups of coleopterans were not sufficiently represented to clearly indicate the effect of overgrazing on their numbers.

(5) In general, Hemiptera increase both in number of species and specimens under conditions produced by overgrazing but are not favored by changes brought

about by erosion following severe over-grazing.

(6) Homoptera show a behavior similar to the Hemiptera in their reaction to overgrazing but show their greatest abundance in somewhat eroded areas.

(7) Among the orthopterans, the Acrididae in most cases are more abundant in heavily grazed areas than in undisturbed prairies but when erosion is severe and changes in plant composition occur, these insects are less abundant than in normal prairie or in grazed but uneroded areas.

(8) Although lightly grazed prairies were found to have a larger number of nesting meadowlarks than undisturbed prairie, heavy grazing produced conditions unfavorable for these birds even though food was abundant. Other birds of the grasslands were not sufficiently abundant to obtain comparative data yet species all seemed to be almost absent in severely overgrazed areas.

(9) Mammals were found to be more or less abundant according to whether the degree of grazing brings about habitat conditions nearer or farther from optimum than the undisturbed prairie.

<div align="center">LITERATURE CITED</div>

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# REVIEWS

## THE INVERTEBRATES [1]

The appearance of Dr. Hyman's first volume of an extensive work planned to summarize existing knowledge of the invertebrates in a form available to most zoologists is a publishing event of importance. Not since the publication of Lankester's *Treatise on Zoology* (never finished) almost forty years ago has a new advanced treatment of this subject been made available in English. The author has rightly relied upon the two great German treatises (Kükenthal-Krumback's *Handbuch der Zoologie* and Bronn's *Klassen und Ordungen des Tierreichs*) for orientation. She has, however, exhaustively combed the world's literature and arrived at her own conclusions on theoretical points.

In the words of the author (p. vii): "The intent of this treatise is to furnish a reasonably complete and modern account of the morphology, physiology, embryology, and biology (sic) of the invertebrates. Classification, phylogeny, and palaeontology are given but brief consideration." Little attention is accorded parasitic forms and the "type" method of presentation, more useful to elementary students has been rejected in order" . . . to give an extensive account of the range of morphological variation to be found within each group."

The general plan and the generous scope of the treatment can be illustrated by the 189 pages which are devoted to the Protozoa. The distribution is: characters of the phylum, 2 pp.; classification, 2.5 pp.; general morphology and physiology, 34 pp. Then each class receives close attention. In the Flagellata, for example, fifteen orders are discussed in 35 pp. and in the whole phylum about four score of genera are mentioned, some re-

peatedly and at length.. Finally there is a compact bibliography of almost 25 pp. Other groups receive comparable treatment. The volume closes with an adequate subject index. There is no index to authors, a weakness which is offset by the fact that throughout the book the documentation is not allowed to come between the reader and the essential subject matter, and by the classified references after each chapter.

Dr. Hyman's ability to write clearly and adequately was already established and the style of this book is simple, direct, lucid, and precise. The terminology is well chosen and happily restricted to the more useful terms, which are clearly defined. This makes the book readable for the general zoologist. As usual she is entirely willing to state her own conclusions on controversial subjects. In this connection we read, p. 16:

Particulate theory has prevailed in biology since the Greeks and at present takes the form of the widely accepted *chromosome-gene* theory. . . . All particulate theories are intellectually unsatisfactory since the very matters for which explanation is sought are attributed without explanation to imaginary particles. A tremendous mass of evidence certainly relates the chromosomes to at least some body characters but it is impossible that the genes alone can be responsible for morphological differentiation, since all body cells contain the same set of genes. The rôle of the genes in morphogenesis remains a total mystery, and in addition the gene theory is difficult to reconcile with the facts of experimental embryology, which show that the fate of a part can be profoundly altered by altering surrounding conditions.

The reviewers agree that particulate theories are unsatisfactory as even approximately "final" solutions. They are useful, however, as working hypotheses in physics and chemistry as well as in biology. Opinions vary widely with regard to the points discussed in the latter part of the paragraph just quoted. Many ecologists share Miss Hyman's skepticism

[1] Hyman, Libbie Henrietta. 1940. The Invertebrates: Protozoa through Ctenophora. McGraw Hill Co., New York. xii + 726 pp., 221 figs. $7.00.

regarding the totipotency of the genes. According to current genetical theory, as we understand it, the genes are no longer thought to be immune from environmental effects. The interaction of genes and influences which are environmental to them, to the containing nucleus, to a given cell, or to the organism itself, is now receiving critical attention from those interested in physiological genetics and in other physiological aspects of development. Sufficient progress has been made so that the claim that: "the rôle of the genes in morphogenesis remains a total mystery" is no longer tenable. In our opinion, one of the interesting modern developments in biology is the growth of a sense of mutual dependence between geneticists and ecologists. This desirable change in attitude is neither reflected nor aided by the position taken in the preceding paragraph.

In another field we read (p. 4) that among the properties of protoplasm there is "the *psychic property* called by some authors *consciousness.*" These words are intended to express that which is known in man as "mind and which biologists believe is traceable through the animal kingdom down to the simplest forms where it probably merges with irritability and modifiability." The reviewers respectfully suggest that it is irritability and modifiability which are the general properties of protoplasm and that "consciousness" is an end-product evolved from these precursors but not necessarily present as such in all protoplasm. Such candid statements add zest to the reading and in no wise detract from the value of the book in its own field.

Dr. Hyman joins the current trend in rejecting both simple mechanistic biology and the vitalism of Driesch. She accepts whole-heartedly the modern organismal viewpoint. The senior reviewer regards this position as one phase of vitalism while the junior reviewer thinks that the mechanism-vitalism problem is outmoded.

The chapter on classification is outstanding. In addition to the usual explanation of taxonomic categories, the more important international rules of zoological nomenclature are listed and there is a hurried but important summary of Linnean and post-Linnean ideas concerning the major divisions of the animal kingdom. This leads to a schematic presentation of a slight variation of the now well-known diphyletic tree which the reviewers regard as being essentially sound. In Dr. Hyman's version, the major dichotomy is represented as coming just after the primitive acoel flatworm level has been reached. Reasons are advanced (p. 694) for disregarding the assumption that a ctenophore-like organism was ancestral to the Bilateria despite the possession of "certain advanced structural features that appear to look forward to the Bilateria."

Miss Hyman's refreshing and penetrating frankness is well illustrated by the following statement (p. 25) with which many ecologists will agree:

The chief difficulties of taxonomy are the impossibility of erecting strict definitions for any given species, genus, etc.; of deciding when any given specimens differ sufficiently to warrant placing them in different species; or of deciding just how much species must differ from each other to constitute different genera; or what characters are most important in making taxonomic distinctions. All such matters are questions of personal opinion on the part of taxonomists, and no rules can be formulated to cover them.

This is the more impressive when we remember that it was written by an experienced practising taxonomist of no mean merit.

There is much ecological material although where labeled it is called "biology," a usage in this connection that is becoming obsolete. Elsewhere the term biology is employed in its usual modern meaning. The kind of ecological material that is presented is indicated by the following examples: Some of the ecological relations of sponges are given, p. 305 ff. The symbiosis of hydroids is discussed briefly, p. 447 ff. The coral reef problem is reviewed and evidence is presented (p. 619)

from recent borings which tends to support Darwin's subsidence theory and, in certain regions, the theory that the reefs grow on submerged banks. Behavior, which, in some ways, is an aspect of ecology, receives a fair amount of attention. More than in most similar books, the invertebrates are treated as animals that live in close relation to their respective environments. The main emphasis, however, is elsewhere and properly so.

The illustrations are unhackneyed drawings from specimens or redrawings from research sources. They are accurate rather than brilliant or dramatic, and

avoid that "noncommital look" which is too often seen. The labeling is said to save space by using numbers in place of the much more convenient direct labeling. Fewer than a dozen illustrations can be regarded as exclusively ecological in interest.

This is a good book. So far as she has gone, Dr. Hyman has succeeded admirably in doing the task she assigned herself. We await the succeeding volumes with confidence tinged with impatience.

<div align="right">
W. C. ALLEE<br>
RALPH BUCHSBAUM
</div>

UNIVERSITY OF CHICAGO

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## PLANT COMPETITION FOR SOIL MOISTURE [1]

Competition in plant communities is recognized as a major influence determining their composition, and the establishment and survival of species and individuals. Without competition environment loses much of its selective action. Competition for soil moisture and to a lesser extent plant nutrients is generally keener than that for light. The authors have assembled further convincing proof of this in the present publication which deals chiefly with the effect of trenching plots in representative forest types of the Piedmont region in North Carolina. It reports the results of six years research on the Duke Forest, augmenting and in large measure confirming the work of Fricke, Fabricius, Toumey, and others, whose results are briefly referred to in the review of literature. A brief description of the climate and of the weather during the experiment brings to light considerable departures from normal in precipitation during the years the plots were under observation, and points out the probable influence of these departures on the reaction of the vegetation.

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[1] Korstian, Clarence F., and Theodore S. Coile. 1938. Plant competition in forest stands. *Bull. 3, Duke University School of Forestry.* 125 pp. 71 figs. Durham, N. C. $1.00.

Seven series of plots were established in second-growth loblolly and shortleaf pine, in two oak types, and in one cove hardwood type in order to "measure the effect of reducing competition for soil moisture and nutrients on the establishment, survival and growth of forest vegetation in five important forest types." Light was to be eliminated as a variable, hence the plots were located as nearly as possible under a closed canopy without including trees forming the main stand in the plots. Milacre plots, one trenched and one control, were established in each case. All roots entering the trenched plots were charted. Unusual pains were taken in refilling the trenches, the soils from each horizon being returned in proper order. Additional A-horizon soil was added to the top from time to time to compensate for settling, and to keep the surface as nearly as possible in its original condition and to avoid affecting the surface drainage. Crown projection maps of circular plots 0.2 acre in area surrounding the trenched quadrats were prepared, and maps of the vegetation on the trenched and control quadrats were made every year.

Analyses of the soils were confined to factors of chief importance to moisture relations—mechanical analysis, moisture

equivalent, and wilting percentage being shown for each horizon. The soils encountered were relatively heavy loams and clays, which thus differed considerably from those existing where other trenched experiments have been made. Thus the loblolly pine plots were on Alamance stony loam, the shortleaf pine on White-store sandy loam, the oak plots on Orange stony loam and Georgeville stony clay respectively, and the yellow poplar stand was classed as Congaree sandy loam, an alluvial deposit from frequent inundation. Interesting comparisons were made between the number of roots of different sizes in each horizon. As was to be expected most of the small roots were in the upper few inches of the soil, and but few in the B and C horizons. The authors believe "that the smallest size class of roots mapped, less than 0.1 inch in diameter, affords a relative measure of absorbing surface." On this basis charts showing the number of small roots per square foot of trench space were drawn, permitting comparisons between the different plots.

Soil samples were taken from each horizon at irregular intervals corresponding to the end of dry periods, just before rain was expected. Sampling was done with a soil auger from the narrow isolation strip around the trenched plot but within the trenched area. No precautions seem to have been taken to insure that roots did not invade the trenched plots anew during the experiment. It seems entirely possible that this may have occurred to some extent in view of the recent findings of Reed [2] that shortleaf and loblolly roots may grow as much as 4 feet per season. In five years this would allow considerable penetration of the plots. Root growth might be even more rapid in the red gum-yellow poplar stand. Analysis of data was based on the null hypothesis, and analysis of variance tables are given for each series of plots for each year. For this purpose the data from all

three horizons were combined. With few exceptions significantly higher soil moisture was found within trenched plots than in their corresponding control plots; in fact ample soil moisture was found in them when conditions in the control plots were critically dry. Analyses of total N, nitrate N and $NH_3$ and organic carbon were made in October 1936 and showed no significant differences between trenched and untrenched plots, even in the case of the five-year-old trenchings. As might be expected, more total nitrogen was present in the red gum-yellow poplar stand where the C/N ratio was 13:1 compared to an average of 21:1 for both trenched and control plots. Slightly larger amounts of total nitrogen were present in trenched plots compared to controls except in one case, but they were not considered large enough to be significant, as was proven by analysis of variance of the data. Measurements with a Weston illuminometer also failed to disclose any significant light intensity differences between trenched and control plots.

The tangible result of the reduced competition of larger surrounding trees for the soil moisture on the trenched plots was displayed of course by the profound changes in the vegetation, and these are well shown by many excellent plates. The characteristics most affected by the trenching were increases in frequency (no. of .01 milacre squares where the plant was represented), total no. of individuals, no. of dry-site individuals, average tree height, no. of individuals per species, and specific density (the total no. of individuals on each plot divided by the frequency). Phytographs, combining all these data plotted on different radii of circles, show the situation on each plot at the end of each year. Many changes were not brought out in these charts, however, but are shown in the actual maps of each plot at different intervals. In some cases a great decrease in the area of the plot occupied by dry-site mosses and lichens occurred as their places were

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[2] *Duke Forest Bull. 4*, reviewed *infra.*

taken by more mesic vegetation. The least change was noted again in the red gum-yellow poplar stand, and it is interesting that the development of advance reproduction of all but the most tolerant species was held back fully as much here as in the oak types. In view of the adequacy of soil moisture on this site the year round and a light intensity of but three per cent of full sunlight, it seems likely that here at least, light was an important factor. The authors suggest that the shortage of radiant energy may have a cumulative effect, in reducing the production of plant food to a point where growth cannot be sustained.

This study supplements previous investigations by confirming through mathematical analysis the already conclusive evidence of the outstanding role of soil moisture, and checking similarly the suspected indirect changes in soil nutrients. Many other trenching experiments were deficient in not investigating the possible influence of other soil factors. Moisture could easily be demonstrated, but questions had been raised whether the increased soil moisture had not brought about other changes, which, rather than moisture *per se* were the direct cause of the observed changes in vegetation. The reviewer recalls, for instance, the lively discussion of this point on the occasion of Professor Henrik Hesselman's visit to Professor J. W. Toumey's trenched plots at Keene, New Hampshire, in 1927. The present observations apparently disprove these suspicions. Among others, the reviewer established a series of trenched plots in a dense old field stand of red spruce in 1925. One of the changes was a pronounced softening of the litter and humus compared to the control plot. Acidity decreased, and the humus became gradually better decomposed and friable. Even if chemical analyses fail to indicate large differences in nitrogen, it is probably true that the activity of micro-organisms (a factor not examined in trenching experiments!) is many times greater in trenched plots, and must inevitably

affect vegetation, even if indirectly. The possibility must also be considered that plants of all kinds growing on the trenched areas absorb nitrogen as soon as it becomes available to them, and therefore it is so promptly removed from the soil that analyses fail to disclose the greater amounts really mobilized. Thus in the experiments reported by Wallihan [3] analyses of leaves "near the end of the growing season showed that plants on the trenched plots had received a significantly greater amount of nitrogen than did those on the check plots," while soil analyses, as in the present study, failed to show such differences. Foliar diagnosis is becoming a more and more useful tool for both the soil scientist and ecologist.

Evidence is increasing that water is the best fertilizer for forests. One is reminded of the numerous cases in Sweden where drainage water from swamps has been allowed to flow over formerly dry, gravelly pine slopes with profound transformation of humus types and truly enormous increases in rate of tree growth; or of the experiments with fertilizers in longleaf pine [4] where the addition of water alone had as great effect as water and fertilizer. Hesselman also was able to modify bad raw humus by watering in northern Sweden.

The authors call attention to the application of their findings to silviculture; where dense stands of pine on dry sites have no surface vegetation, exclusive of xeric mosses and lichens, such a condition can often be regarded as an indication of need for thinning. This statement is qualified as applying to Piedmont conditions. There are abundant examples of open, *understocked* stands on dry sites with only moss and lichen vegetation in many parts of the world. Such absence

[3] **Wallihan, Ellis F.** Factors affecting the response of forest vegetation to trenching. *Jour. For.* **38**: 223–224, 1940.

[4] **Paul, Benson H., and Ralph O. Marts.** Controlling the proportion of summerwood in longleaf pine. *Jour. For.* **29**: 784–796, 1931.

of vegetation may arise from disturbances by fire and lumbering, lack of seed supply, over-grazing, and the like, or may be due to extreme moisture deficiency. No general rule can be made. Conversely, a rich and dense forest floor flora does not mean that no thinning is needed. Physical growing space may be so crowded that the trees cannot expand their crowns to increase assimiliation (a necessary preliminary to increased diameter growth), even

if no marked competition for soil moisture can be demonstrated. This is recognized by the authors in commenting on the red gum-yellow poplar cove. The bulletin is well-published and carefully proof read, in keeping with the high standard of this series of studies in fundamental and applied ecology.

HENRY I. BALDWIN

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## THE NATURAL HISTORY OF SOUTH AMERICA [1]

Through somewhat fortuitous circumstances a number of very great men took part in the scientific exploration of South America, and since their observations and studies played no small part in making them great, some comparative examination of the published accounts of their travels could scarcely fail to be interesting and fruitful. It is thus with high hopes that naturalists will turn to a book about the explorations of the great naturalists in South America, expecting to refresh their memories about the work of such men as Humboldt, Darwin, Wallace, Agassiz, and Bates, to learn something of their historical significance, and perhaps to catch some reflection of the stimulus from the personalities that so profoundly impressed their contemporaries.

It is disappointing to report that Dr. Cutright's book does not have such ends in view. It quite simply catalogues the naturalist explorers of South America, with but little difference of emphasis for scientists like Darwin and Humboldt, for collectors like Cherrie or Miller, or for literary men such as Hudson and Beebe. This introductory section occupies only forty-one pages. It may be noted with regret that the rather full bibliographic list, by being limited to books, and to

[1] Cutright, P. R. 1940. The Great Naturalists Explore South America. *The Macmillan Co., New York.* xii + 340 pp. 31 pls. $3.50.

books in English, misses the references to such important modern explorations as those of G. H. H. Tate, which are excellently reported in the *Geographical Review*, and to Hans Böker's Tiere in Brasilien. The significance of Böker's book may be grasped from his remarkable subsequent studies on comparative biological anatomy. Of the older naturalist collectors who did write books, H. H. Smith is omitted.

The rest of the book is a compilation of what has been written by the naturalists mentioned in the introductory section about various notable animals of South America, with some descriptive natural history from standard sources thrown in for good measure. Some of these animals are dealt with as single species, like the tapir, the jaguar, or the hoatzin. Other short chapters deal with inclusive groups like "rodents," "monkeys," or "turtles." The illustrations are for the most part excellent, though the zoologist will recognize many of them as old friends. This section of the book may be genuinely interesting to the non-zoologist. The book will, in fact, be invaluable to zoologists for recommendation to their traveller friends who may be going to South America.

It cannot be detected from the book that Dr. Cutright's account of the natural history of tropical America represents more than an arm-chair interest. It is

thus not especially surprising to find Hudson's gaucho stories accepted as authentic natural history. To miss the fact that Hudson was not a naturalist but an artist is to do him a grave injustice. Far Away and Long Ago is pure poetry, perhaps more deeply true than many a catalogue of facts; but the natural history of The Naturalist in La Plata is of quite a different order from the factual reporting of a Bates.

Gratifying as it is to have some report of the modern successors of the great naturalist explorers of the nineteenth century, it is a kind of sacrilege to admit such unmitigated frauds as Up de Graff and von Hagen to the same pages with genuinely great and significant men, of whom there is no dearth even among the moderns.

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## DESERT WILD FLOWERS [1]

The author refers to this book as a "pocket picture-book herbarium." It is intended primarily as a field reference book, not only for "schooled professional and amateur botanists," but also for travelers and out-of-doorists. "Cattlemen, ornithologists, bee-keepers, agriculturists, and allergists will all find their special interests amply regarded throughout the pages. Text and drawings are designed to facilitate quick identification of the plants, no matter what the user of the book may be or where his interests may lie."

Practically all known plants of the deserts of California and related portions

of Nevada are included, many of which have never before been illustrated. The author has assigned English names to plants that have had no "common" name, and special attention has been given to the "natural history" of the plants rather than to their description. The meanings of the scientific names are given, and there are brief accounts of more than 1 experiments commemorated in bota of pine

The book is almost alone in its field, and will undoubtedly meet with a warm welcome.

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## PROBLEMS OF LAKE BIOLOGY [1]

The fresh water lake, with its varied fauna and flora, is not improperly regarded as a microcosm whose characteristics are a consequence of the competing

and coöperating life within it and of the physical and chemical factors which determine the kind and numbers of organisms present. In some respects it is worth while to go even further than this, to regard the lake as a living unit analogous, perhaps, to a complex multicellular organism in which the successive and cyclic transformations of organic matter constitute a physiology or metabolism subject to the vicissitudes of age, environment and the like.

This symposium, organized by the

Limnological Society of America and published by the American Association for the Advancement of Science under the title Problems of Lake Biology, takes these broad concepts as a basis upon which a series of distinguished contributors have presented discussions of the current states of knowledge in their respective fields of activity. A variety of interests are represented, ranging from the geological, physical and chemical factors to the bacteria, plankton and higher animals and plants that inhabit these bodies of water. The physical and chemical aspects of the lake are discussed by D. S. Rawson and the problems involved in the absorption and utilization of radiant energy by G. L. Clarke. The relations of the phytoplankton and the zoöplankton to aquatic biology are presented by G. W. Prescott and by W. L. Tressler and the relatively new subject of lake bacteriology is reviewed by A. T. Henrici. The fauna of the beach and lake bottoms are discussed by R. W. Pennak and by F. E. Eggleton, the rooted plants by L. R. Wilson and the fish and higher animals by F. E. J. Fry.

Of these discussions the ecologist will find those of Dr. Clarke and of Dr. Henrici of particular value because they represent fields in which there has been unusual activity in recent years. The development of the photocell has made possible relatively accurate quantitative measurement of the penetration of light into bodies of water and has been utilized for this purpose by Birge, Juday and others in the study of fresh water lakes and by Clarke and his co-workers at Woods Hole. Clarke includes a considerable amount of quantitative data in the form of graphs that will be of no small interest in connection with the distribution of phytoplankton.

The inclusion of Dr. Henrici's competent and detailed discussion of the lake bacteria is of particular significance. Although the place of these microörganisms in aquatic biology has long been recognized, the water bacteria have remained unknown not only to the limnologist but also to the conventional bacteriologist whose interests in water bacteriology are generally confined to its sanitary aspects. Only in recent years has this subject been systematically investigated. Largely through the work of Waksman at Woods Hole and Zobell at La Jolla on bacteria in the sea and coastal waters and the extensive studies of Henrici on fresh water lakes, the fragmentary information previously available has been extended and at present is being consolidated to form a solid foundation for future work. It is becoming increasingly apparent that the bacteria, long known as integral and indispensable factors in the economy of the soil, occupy an equally important place in the metabolism of bodies of water. It is a source of mild surprise to the reviewer that as yet there has been no consideration of the intestinal flora of fish, a point on which information is almost completely lacking.

Characteristic of the symposium is the frank and critical appraisal of current knowledge as a determinant of the more promising lines of future investigation. Peculiarly valuable to workers in allied fields, such discussion is perhaps even more informative, albeit in a somewhat subtle fashion, than the detailed survey of the literature that comprises the review. In view of the diversity of interests represented in lake biology, the essential unanimity of opinion evident in this volume is altogether gratifying. Although it is frequently, and by now tritely, said that the relative maturity of a science is indicated by the extent of its quantification, in the reviewer's opinion an equally significant evidence of a coming of age is the broadening of the specialist's view such that he is able to appreciate and assess the significance of his own field of investigation to the broader biological problems.

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## West Virginia Liverworts [1]

The Hepaticae have been conspicuously neglected in North America. Aside from lists and keys with extremely local application, there are only four or five regions which are covered adequately by existing manuals. Notable among the latter are Connecticut, Pennsylvania, Florida, and the Northwest. The new manual for West Virginia fills a distinct need.

The liverwort flora of West Virginia includes 111 species, according to Dr. Ammons. The species are keyed, illustrated, and described. The keys are based on vegetative characters, which increases their usefulness considerably. Descriptions are full, including measurements of leaf cells and spores. For each species is given synonymy, habitat, distribution both in the counties of West Virginia and in North America, and aids to identification. Species are illustrated with line drawings, those of the leafy liverworts being particularly satisfactory. All drawings are to the same scale; this is no doubt a great convenience, but it makes the habit sketches ($\times$ 3) of a few species too small to be of much value for anatomical details.

Much useful information is given in the appendices. There is a list of derivations of species names which will be of interest to those who are acquainted only with the names of seed plants. The list of authorities' names, many of whom are commonly known only as abbreviations, is a survey of eminent workers in this field. The glossary is not illustrated, but terms of restricted use are referred to particular illustrations of species. The bibliography is more than adequate; be-

sides works cited in the text, reference is made to general manuals, and papers on morphology.

The importance of a knowledge of bryophytes is recognized by European plant ecologists, but has not received so much attention in America. (For example, a cursory examination of the index of Braun-Blanquet's *Plant Sociology* reveals over 75 scientific names of bryophytes, while Weaver and Clements' *Plant Ecology* mentions less than a dozen). Such references as there are in American ecological literature are to a "moss stage" in succession, or a ground cover of "mosses." With a few important exceptions, the relationships between them and their relationships with higher plants, their value as indicators of habitat conditions, and even their names, are omitted. The work being done at present by Steere [2] on the distribution of mosses, and by Sharp and Cain [3] on moss sociology, indicate that the general ecologist could make good use of these plants.

Dr. Ammons has provided enough explanatory material to enable the ecologist to identify the liverworts of this region; more ecological material might well have been included, and summaries of habitats, associations, and the geographic affinities of the flora would be desirable. The purpose of the book is, however, taxonomic, and on taxonomic grounds it is a valuable contribution.

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[1] Ammons, Nelle. 1940. *A manual of the liverworts of West Virginia*. 164 pp., 26 pl. Notre Dame, Ind., American Midland Naturalist. $1.75.

[2] Steere, W. C. 1937. Critical bryophytes from the Keweenaw peninsula. *Rhodora* 39: 1–13; 33–45.

[3] Cain, S. A., and A. J. Sharp. 1938. Bryophytic unions of certain forest types of the Great Smoky Mountains. *Amer. Midl. Nat.* 20: 249–310.

## North American Mammals [1]

Hamilton has condensed into this book on American mammals a brief summary of the existing information about the North American members of this important class of vertebrates. The point of view throughout is that of the field naturalist.

The material for the book has in general been well selected and it is presented in an interesting manner, reflecting the enthusiasm of the author for his subject. The ecologist will be most interested in the chapters on adaptations, foods, storage, reproduction and early life, the home of mammals, hibernation, migration, mammal populations, behavior, distribution, useful mammals, injurious mammals, and predatory mammals. The ecologically important subject of ecological communities has been treated only in a single paragraph, which deals with the biome.

Some of the statements made by the author seem to the reviewer to be over-inclusive and to go beyond the available evidence. It has not been proved, for instance, that "The changes which have taken place in the organization of water-living mammals vary in direct ratio to the time during which the influence of the water has been operating " (p. 97).

The declaration on page 111 that in the desert areas of the West "there is often no rain, snow, or dew for months or even years at a time," is an overstatement. It may also be doubted that "some species have never learned to drink" (p. 112). In semi-deserts only a few species of mammals remain dormant from July to late winter, and not all kinds, as might erroneously be inferred from the discussion on page 113. In the mountains *Lepus washingtonii* assumes a white coat

in winter,[2] though in the lowlands it does remain brown all year (p. 74).

The statement on page 71 that "The coat color of most small mammals tends to approximate the color of the environment," seems to be irreconcilable with the conclusion on page 72 that "climatic factors, rather than the optical properties of the background, appear to be responsible for the differences of color between the mountainous and desert country."

The rump-flash of the antelope jack rabbit may not be a "fine example of directive coloration" (p. 73), for this conclusion is not supported by the studies of Vorhies and Taylor,[3] who are in doubt as to the usefulness of the habit.

Among minor errors which evidently are due to incorrect transcription are the statements that "the reptiles possess both a right and left aortic arch, imperfectly connected" (p. 62), and "Aquatic mammals of the boreal regions must develop a thick layer of subcutaneous fat to inoculate them against the cold" (p. 109).

A short "bibliography," which actually is a list of literature cited, is given at the end of each chapter. In the experience of the reviewer these scattered lists are difficult to use, and a more complete bibliography at the end of the book would have been more desirable.

The excellent ink sketches by Lloyd Sandford add much to the interest of the book, but the drawing of the saber-tooth tiger (fig. 10) is poor. There are a number of photographs, most of which are good, but a few, notably those reproduced as figures 31, 65, and 80, are inferior in quality.

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[1] Hamilton, W. J., Jr. 1939. American Mammals; their Lives, Habits, and Economic Relations. *McGraw-Hill Book Co., New York and London.* xii + 434 pp. 92 figs. $3.75.

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[2] **Taylor, W. P., and W. T. Shaw.** 1927. Mammals and birds of Mount Rainier National Park. *U. S. Natl. Park Service,* p. 115.

[3] **Vorhies, Charles T., and Walter P. Taylor.** 1933. The life histories and ecology of jack rabbits, *Lepus alleni* and *Lepus californicus* ssp., in relation to grazing in Arizona. *Univ. Ariz. Agric. Exp. Sta. Tech. Bull.* **49**, p. 489.

Some of the most valuable chapters to the ecologist are those which deal with the food of mammals and with the relations between predators and prey. This is a field in which Hamilton is a recognized authority. Almost all field biologists are in agreement with the position taken by him that control measures are necessary where mammals become pests affecting crops or domestic live-stock. It also will be generally agreed that the control measures employed and the individuals chosen for the work have in the past not always

been wisely selected, though many mammalogists would consider this to be an understatement. The author emphasizes the complexity of the predator-prey relationship and the desirability of much additional study of this ecologic and economic problem.

The book is heartily recommended to all ecologists interested or concerned in any way with mammals.

LEE R. DICE

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## THE EXPANDING PLANT [1]

The course of root and shoot growth in trees is of especial interest since trees are such long-lived perennials, and extensions made in both roots and tops are usually permanent and cumulative. Expansion of the food-absorbing and assimilating parts must precede growth in the trunk. Cambial growth has received greater attention. The bulletin considered here reports results of root and shoot growth of shortleaf and loblolly pines as correlated with air temperature and soil moisture especially. It is in the correlation with climatic factors that the author attempts to overcome the shortcomings of some similar studies.

Twenty-five trees of each species were observed in a 6-year-old natural stand growing on a sandy loam soil at Durham, North Carolina. Soil sampling revealed no marked differences throughout the area studied. Root elongation was measured by periodically excavating and then recovering two lateral roots on each tree, identified by small pegs, which were used also as reference points for measurements. Height growth was simpler, a steel tape being hooked to a small nail driven into the main axis of the tree, and

the distance to the growing tip measured. Therefore it is not surprising that the interval between measurements of root activity varied from 7 to 50.days (the latter from Nov. to Jan.) and from 2 to 12 days for shoot growth. Observations extended over 17 months beginning in the spring of 1935. Soil samples ($A_2$ horizon only, where roots were located) were taken at frequent intervals both before and after the rains, and moisture content and wilting percentage determined. Soil and air temperatures were recorded continuously, and records of evaporation and precipitation kept. All climatic factors were measured in the stand and at the height where growth was taking place.

Roots were found to make some growth practically the year round with a maximum rate in April and May and minimum in January and February although the differences were not startling in amount. The average total growth of loblolly pine roots April 1935 to August 1936 was 47.4 in. and 26.2 in. for shortleaf. Shoot growth averaged 27.7 in. and 21.5 in. in 1935 and 39.4 and 25.9 in. for 1936 respectively. The curves of both root and shoot growth were essentially similar for both species. The data were examined critically by the analysis of variance method, and no significant relation between root growth and environmental factors found. There were indications,

[1] Reed, J. F. 1939. Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. *Bull. 4, Duke University, School of Forestry.* 7 fig. 52 pp. Price $.50.

however, that deficient soil moisture during the summer and low soil temperature during the winter may reduce growth. Shoot growth was definitely correlated with temperature; in fact an increase of each unit of physiological temperature index (described by Lehenbauer '14, but not explained in this bulletin) resulted in an average of 1.4 per cent increase in daily height growth. Height growth took place over about five months, a far longer period than reported for trees in the north. This raises many interesting questions. Growth seems to begin in all parts of the country as soon as air temperature is high enough over a period of a week to 10 days to set growth forces in action, but no cause for cessation of shoot growth when all environmental factors are still favorable for rapid elongation has been shown, nor does the present publication elucidate that point. The same is true to lesser degree of root growth. MacDougal '38 [2] presents no data to explain fluctuations of root growth in *Citrus* but states (p. 217) : "The initiation of root-elongation was probably influenced to some extent by soil temperature, but the cessation in summer was certainly not due to low temperatures. It seems impossible at present to explain the cyclic growth of roots on any simple basis although it was probably affected by temperature and hormonic communication between root and shoot." Similarly photoperiodic controls have been suggested as influential in causing cessation of height growth, and the photoperiod has been shown to influence vegetative growth in other plants. Complete explanation of this behavior apparently awaits experiments in which the trees are grown in a controlled and artificially manipulated environment.

For 21 days during June and July height growth measurements were made twice daily, at 6:30 A.M. and 6:30 P.M. More than double as much growth oc-

[2] **MacDougal, D. T.** 1939. *Tree Growth.* Chronica Botanica Pub. Co., Leiden, Holland.

curred at night as by day, loblolly pine growing at the surprising *average* rate of 3.21 in. per night during the 21 days. The differences between day and night growth correlated most strongly with the differential evaporation rate of night to day, indicating that reduction in transpiration was the principal cause of greater growth by night. No attempts were made to investigate the possible stunting effect of light compared to darkness, which would have required enclosing the trees in controlled humidity chambers, with one shaded and one unshaded.

A close interrelation was noted between root and shoot growth. While root growth continued during all 12 months of the year and shoot growth only for five months, about 78 per cent of the former occurred during these five months of shoot growth. Both root and shoot growth reached "their first seasonal peak almost simultaneously in April or May." The author cites previous investigators as concluding that this period comes when not only soil moisture is abundant, and temperature rising, but that there is a large amount of stored food available. In the present study, however, the data in fig. 1 show total soil moisture to have been at the lowest point in the whole course of the experiments in April and May 1936 and during half of the latter month below the wilting percentage, while a definite peak of root growth occurred (fig. 3) during this period. A similar peak occurred the previous year with, however, rather adequate (but not the highest) soil moisture. These are illustrations of the failure of root growth and soil moisture to parallel each other.

An interesting observation was that two to five whorls of branches were formed by these pines in one year's growing season, showing that counting whorls is an unreliable method for age determination in these species and in this climate. Northern pines rarely if ever form double whorls in one season. Is this a characteristic of the species only, or does the same species tend to develop

lateral buds more profusely in southern parts of its range? The long growing season, and possibly fluctuations during its course may have given stimulus to these side shoots.

This study represents a painstaking evaluation of the environmental influences on root and shoot growth of trees growing under natural conditions and undisturbed (except for occasional uncovering of a negligible fraction of the root system). The results are highly interesting to ecologists, but they fail to answer the question why—in regard to many aspects of growth. Mathematical analysis of the observed environmental data and growth measurements were relied upon almost wholly for explanations. It would seem as if control of some at least of the factors of environment must be the next step in explaining the reasons for the obviously complex phenomena of periodic growth in trees.

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## WILDFOWL FOOD PLANTS [1]

In this publication McAtee has summarized the vast amount of information concerning the food of waterfowl which he has compiled during his tenure in the United States Bureau of Biological Survey. In treating the available data upon this subject, the author has presented a systematic discussion of the various families of aquatic plants that are utilized as waterfowl foods, and has, upon the basis of field investigations and laboratory analyses of the contents of waterfowl stomachs, indicated the relative importance of each of these groups in the diet of wildfowl.

The book also considers various ecological aspects of the distribution of aquatic plants, and discusses the depth requirements and the limitations of light intensity, alkalinity, acidity, and salinity of many of the more important species.

The author has utilized the method of presenting in tabular form much of the data relating to habitat preferences, limits of environmental resistance, transplantable parts, etc., of the more important of the natural waterfowl food plants, and has in this way added materially to the value of this guide by making these data readily available to those engaged in the practical aspects of managing wildfowl refuges and hunting areas.

Finally, McAtee has given many practical suggestions for diking fresh and salt water marshes, and for transplanting duck foods to suitable habitats in order to make these localities more attractive to wildfowl. He has thus made this manual one of considerable value for hunters, conservationists, owners of private refuges, and ecologists who are interested in the perpetuation of an optimum number of these waterfowl for the purposes and benefit of·man.

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[1] McAtee, W. L. 1939. Wildfowl Food Plants—Their Value, Propagation, and Management. *Collegiate Press, Inc., Ames, Iowa.* ix + 141 pp. 4 figs., 11 plates. $1.50.

# BOOK NOTICES

**Burlingame, L. L.** 1940. Heredity and social problems. xi + 369 pp. 77 figs. *Mc-Graw-Hill Company. New York.* $3.50. This book grew out of a course given at Stanford University designed to correlate the social with the biological sciences. The aims of the book are well stated in the preface and may be reproduced here: "The principal aims have been (1) to present a brief and simple introduction to the biology of reproduction and its consequence, heredity; (2) to show how and when this knowledge can or cannot be applied to social problems in the broader sense; (3) to acquaint the biology student with the possible practical applications of his science to human affairs; (4) in particular to set forth as clearly as possible the way in which heredity and environment jointly control the development of organisms, including man, and to contribute towards dispelling the common popular misconception that these two sets of factors are opposed or mutually exclusive; (5) to show how changes in birth and death rates, immigration, war, and differential fertility alter the genetic composition of populations; (6) to show what methods are practicable to alter the rate or direction of any of these changes that society may think necessary or desirable; (7) to indicate the bearing of genetics on education and the theories and practices of government."

This is a useful compilation and synthesis of a mass of interesting information.

**Fox, Irving.** 1940. Fleas of Eastern United States. *Iowa State College Press, Ames, Iowa.* 166 figs., 191 pp. $3.00. This is a well organized taxonomic publication with a pleasing format and adequate drawings. Fifty-five species of fleas are described and classified in five families and thirty-three genera. Localities and host species are listed and a host index is included. Notes on collecting, morphology, life history and control make up the introduction. A selected bibliography is attached. Nearly all the host species of birds and mammals harbor more than one species of flea and each species of flea usually is to be found on several host species. However, there are a few cases of host-parasite specificity.

**Strong, Reuben Myron.** 1939. A Bibliography of Birds. Zoölogical Series, *Field Museum of Natural History,* 25, Parts 1 and 2. Publication 442 and 457. 937 pages. $11.00 for both parts. Professor Strong and the Field Museum are to be congratulated on producing an admirable author index in Parts 1 and 2 of "A Bibliography of Birds." Part 3, now in press, will arrange bird literature according to subject matter. Happily, ornithology has been interpreted in a broad biological sense and the reader finds references to the following aspects of the subject: anatomy, behavior, biochemistry, embryology, pathology, physiology, genetics, ecology, agriculture, economic ornithology, poultry culture and evolution. Although bird taxonomy and distribution are not emphasized, a number of key references in this field are included. Each citation consists of author, date of publication, title, journal (or publishing house), volume and page reference. The citations are arranged alphabetically by senior author and junior author and chronologically under the author. Professor Strong provides an interesting polemic in the preface where he states: "It was not easy to select ecological references, because of the difficulty of deciding what are contributions to ecology. Articles written by ecologists were accepted, and titles sent by ornithologists which they classed as ecological were also accepted. A number of publications which have ecological bearings, though obviously not written with a clear-cut ecological viewpoint, were also included. All of these were indexed under ecology."

**Archbold, Richard, and A. L. Rand.** February 24, 1940. New Guinea Expedition, Fly River Area, 1936–1937. *Robert M. McBride and Co., New York.* xviii + 206 pp., illus. $3.50. In this narrative of an expedition to southern New Guinea there are included many notes on vegetation, on the native peoples, and on the birds, and less frequent observations on the other animals. The ecological data are scattered through the book and no attempt is made to present a description of the ecology of any part of the area.

**Eales, N. B.** 1939. The littoral fauna of Great Britain. A handbook for collectors. *Cambridge University Press.* xvi + 301 pp. 24 plates. $3.50. As the sub-title implies this book has been designed to meet the needs of students specializing on the ecology of areas between tide marks. The approach is largely taxonomic and there are a number of excellent keys. There is also a good bit of habitat data. The book should be very useful to British biologists. It will also be valuable to American workers in a more general sort of way. A cordially recommended volume.

Studies in the Mecoptera. (1) **Setty, L. R.** Biology and morphology of some North American Bittacidae. (2) **Cooper, K. W.** The genital anatomy and mating behavior of *Boreus brumalis.* Appearing in, *The American Midland Naturalist* 23: 257–367 (published sep-

arately as a monograph). These appear to be two well-done studies on the anatomy and general ecology of certain American mecoptera. The papers contain much of interest to the specialist and have enough interest for the general ecologist to warrant mention in these columns.

**Carr, Archie F.** 1940. A contribution to the herpetology of Florida. *Univ. Fla. Publi-* *cation* **3** (1). 118 pp. $1.35 (paper bound). This book should be useful to herpetologists collecting in the southeast. It appears to be a competent survey of the taxonomy of the reptiles and amphibia of that area with good keys for the determination of specimens. The volume contains the following six chapters: Introduction, Derivation of the fauna, Habitat distribution, Keys, Annotated list, Bibliography and Index.

# NOTES AND COMMENT

## Our New Format

The January, 1940, issue of Ecology is the first number to appear in double column format. There was also a change in paper stock. The change in format was adopted primarily for the purpose of enabling the journal to publish more reading matter, and to publish more promptly, without increasing the cost of publication. In addition to rendering the bill for this number as it is (new format), the printers kindly rendered an itemized bill to show what it would have cost to produce this issue in the old, one-column-to-the-page, format, including only the pages of reading matter. The net total amount of saving is $70.50. We published 111 pages of reading matter averaging about 640 words per page, or a total of 71,040 words. The January, 1939, issue had 110 pages averaging 510 words each (130 less words per page), a total of 56,100 words. Thus the new format and one additional page gave 14,940 more words of reading matter.

The January, 1939, number had more engravings than the January, 1940, issue. If, from the total cost of each issue, we deduct the cost of the engravings and also a small non-recurring item involved in the change of format, we find that the change of format and paper stock has given us 26.6 per cent more reading matter at an increased cost of only 12 per cent. Tests have shown that matter set two columns to the page may be more rapidly read, and with less eye-strain, than when set one column to the page. As stated above, we are also able to publish papers more promptly in the new format which contains more per page. Thus the new format and paper stock give our readers three advantages.

C. Stuart Gager

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## Factors Influencing the Survival of the Fasting Fresh Water Oligochaete, Tubifex, in the Laboratory

The possibility that the fresh-water Oligochaete, *Tubifex tubifex*, might serve as a valuable pharmacologic test object led us to investigate some of the factors influencing its survival in aqueous media in the laboratory. Stone's studies ('32, '33) on the regeneration of *T. tubifex* disclosed the fact that these worms will live in the tap water of Columbia, Missouri, and of Philadelphia, Pennsylvania. Our own experience has shown that unless the tap water of New Orleans, Louisiana, is previously boiled, Tubifex will not survive in it.

Analyses of the tap water of Columbia showed it to be a very hard water of pH 8.0 and containing no active chlorine. The tap water of New Orleans is soft, low in dissolved constituents, and of pH 9.5 to 10.0. The minimum chlorine content is 0.7 parts per million, but the value is occasionally slightly higher. The chlorine content of the water is stabilized by the addition of $(NH_4)_2SO_4$. The tap water of Philadelphia was intermediate between those of New Orleans and Columbia in dissolved constituents; it possessed a pH of 7.1 and a chlorine content of 0.1 parts per million at the time of Stone's experiments.

Consideration of the contrast between these tap waters, one of which, that of New Orleans, was lethal to Tubifex, caused us to study the effects of chlorine, of varying pH, and miscellaneous ions upon the survival of the worms.

### Experimental

Good distilled water (not redistilled) of pH 5.5 was found to be compatible with the survival of Tubifex. We have observed that as little as 100 cc. of distilled water contained in open crystalizing dishes 9 cm. in diameter presenting a surface of 64 sq. cm. fulfils the low oxygen requirements (unpublished data) of about 20 worms, providing the water is frequently changed.

In some experiments preliminary anesthesia was required to clean and sort the worms. Anesthesia with chloretone (0.2 per cent) lasting less than ten minutes was induced and terminated several hours before the experiments. Our experience indicates that much longer periods of chloretone anesthesia do not damage Tubifex appreciably. Stone ('32), also, has observed that pre-treatment with chloretone does not modify the regenerative response in Tubifex. Child and Rulon ('36), however, observed that even smaller concentrations of chloretone modified the ability of Tubifex to react with certain dyes. They suggested the possibility of additive action between the dyes and the narcotic. All our experiments were carried out with fasting animals.

In the first series of experiments the toxicity of HOCl to Tubifex was studied. Worms were placed in solutions which contained HOCl in concentrations equivalent to concentrations of

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elementary chlorine in the range 0.4 to 12 parts per million at a pH of 5.5. Distilled water, redistilled over $Na_2S_2O_3$ to remove active chlorine, was used to prepare the solutions. About 10 worms were placed in 100 cc. of the liquid in each beaker, and the observations herein reported are derived from experiments in which approximately 700 worms were used. The criterion for lethal toxicity was arbitrarily set as that concentration which killed all animals in 18 hours. It was observed that Tubifex does not survive in concentrations above 0.6 parts per million of elementary chlorine (0.0000085 molar $Cl_2$) in the form of HOCl. Examination of the animals which died revealed that death was apparently preceded by the imbibition of water and the production of turgor, followed by blanching. Their complete disintegration followed quickly after death.

In the second series the toxicity of chlorine was compared with that of chloramines. Varying concentrations of chloramines were produced in the experimental beakers by adding $(NH_4)_2SO_4$ to HOCl. The HOCl was derived from NaOCl; in the medium of distilled water HOCl is liberated. Following the mixing of HOCl and $(NH_4)_2SO_4$ two hours were allowed to elapse, to permit the formation of chloramines before adding the worms. At the experimental pH, 5.5, there is, according to Chapin ('29), a tendency to the production of dichloramine, $NHCl_2$, in the presence of unquestioned excess of ammonium ion.

To guard against the introduction of ammonium sulfate in concentrations intrinsically lethal to Tubifex, a fact to be dealt with subsequently in this paper, ammonium sulfate was added, not in excess, but in concentrations equivalent to HOCl in the dichloramine sense. Such concentrations would not effect complete conversion of the HOCl present to dichloramine, but they would produce sufficient quantities of dichloramine to exert some toxic action if such be existent. It was observed that Tubifex survived just as well in concentrations of HOCl to which $(NH_4)_2SO_4$ stoichiometrically equivalent to dichloramine production had been added, as in solutions of HOCl of equivalent strength; that is they survived equally well in concentrations of HOCl equivalent to 0.6 parts per million of elementary chlorine (0.0000085 molar $Cl_2$) whether or not $(NH_4)_2SO_4$ was added. These results indicate that the toxicity of chlorine as chloramines, and its toxicity as HOCl, a compound to which chloramines may be hydrolyzed, do not differ appreciably.

Because it was necessary to add ammonium sulfate to HOCl to produce chloramines in the test solutions, control experiments were provided to test the intrinsic toxicity of $(NH_4)_2SO_4$ and its component ions. These experiments involved the use of $(NH_4)_2SO_4$, $NH_4Cl$, and

$Na_2SO_4$. It was observed that Tubifex survives in concentrations of $(NH_4)_2SO_4$ below approximately 20 parts per million of ammonia nitrogen (0.0014 molar ammonium ion); in concentrations of $NH_4Cl$ below 30 parts per million of ammonia nitrogen (0.002 molar ammonium ion); and in concentrations of $Na_2SO_4$ well above 390 parts per million of sulfate ion (0.0039 molar sulfate ion). Inasmuch as Tubifex survived in concentrations of sodium ion and chloride ion as high as 6500 parts per million of NaCl (0.11 molar), the toxicity apparently lies in the ammonium ion. In those experiments in which $(NH_4)_2SO_4$ was added to HOCl solutions to produce chloramines, the concentrations of ammonium ion were always kept far below the toxic limits, the highest being one half part per million of ammonia nitrogen (table I).

TABLE I. *Concentrations of substances above which* T. tubifex *does not survive. Temperature range: 25°–28° C.*

| $Cl_2$ as HOCl | $(NH_4)_2SO_4$ | $NH_4Cl$ | Chloramines |
|---|---|---|---|
| 0.6 p.p.m. of $Cl_2$ | 20 p.p.m. of $NH_3$-N | 30 p.p.m. of $NH_3$-N | 0.6 p.p.m. of $Cl_2$ |
| $Na_2SO_4$ | $NH_4Cl$ in diluted Ringer's solution | $Cl_2$, as HOCl, in diluted Ringer's solution | $Na_2SO_4$ in diluted Ringer's solution |
| Above 390 p.p.m. of sulfate ion | Above 110 p.p.m. of $NH_3$-N | 0.6 p.p.m. of $Cl_2$ | Above 390 p.p.m. of sulfate ion |

Attempts to study survival in phosphate buffered solutions presented the interesting possibility that phosphate ion is toxic to Tubifex. To determine whether the toxicity of phosphate is related to hydrogen ion concentration, the animals were placed in solutions prepared to produce series of concentrations of phosphate ion from 0.0006 molar to 0.08 molar. Each series of graded phosphate concentration was adjusted to the same pH, the range from pH 4.6 to pH 8.4 being covered. About 10 worms were placed in each container. Death of all worms at the end of 18 hours was considered as the end point. In concentrations immediately below the end point, however, the animals were usually in a definitely moribund state. These results show clearly that the toxicity of phosphate ion to Tubifex is intensified by increase of pH (table II).

Death of the worms from toxic concentrations of ammonium ion and from phosphate ion

TABLE II. *Relation of pH to concentration of phosphate lethal to Tubifex*

| Phosphate concentration | pH | | | | | | |
|---|---|---|---|---|---|---|---|
| | 8.4 | 7.8 | 7.5 | 6.6 | 6.1 | 5.2 | 4.8 |
| 0.08M | D | D | D | D | D | D | D |
| 0.04M | D | D | D | D | D | L | L |
| 0.02M | D | D | D | D | D | L | L |
| 0.01M | D | D | D | L | L | L | L |
| 0.005M | L | L | L | L | L | L | L |
| 0.0025M | L | L | L | L | L | L | L |
| 0.0012M | L | L | L | L | L | L | L |
| 0.0006M | L | L | L | L | L | L | L |

D = Death of all worms.
L = Some life persisting.

is characterized by cessation of movements, unaccompanied by the imbibition of water and blanching, characteristic of death from chlorine. Blanching and disintegration, obviously, supervene eventually.

It was observed that Tubifex survives quite well in good distilled water and also in mixtures of distilled water and amphibian Ringer's solution [1] made up stepwise in concentrations of 0 per cent Ringer's—100 per cent distilled water to 100 per cent Ringer's solution—0 per cent distilled water. This series represents a pH range of 5.5 to 7.5. During these observations the media were changed daily. In certain cases the animals lived without food for periods as long as one month under the foregoing conditions.

Experiments were also conducted to test the influence of the ions of amphibian Ringer's solution diluted with an equal volume of water and adjusted to pH 5.5 on the toxicity of those ions already found to be toxic to Tubifex in distilled water. This concentration was chosen because it presented an apparent superiority to distilled water in experiments on regeneration which we have not yet published. It was observed that the ions of diluted Ringer's solution did not modify the toxicity of phosphate ion or of HOCl. The toxicity of ammonium chloride, however, was diminished by the presence of those ions. Even 110 parts per million of ammonia nitrogen failed to kill the worms in a period in which 30 parts per million ammonia nitrogen as NH₄Cl dissolved in distilled water were lethal. The relatively minor toxicity of sulfate ion was diminished by the presence of the ions of diluted amphibian Ringer's solution.

[1] Composition of amphibian Ringer's solution: NaCl—0.65 per cent; KCl—0.014 per cent; NaHCO₃—0.010 per cent; CaCl₂—0.015 per cent.

### DISCUSSION

The addition of ammonium salts to chlorinated tap water to insure the retention of chlorine produces chloramines which are more stable than hypochlorous acid. Since active chlorine in very small concentrations is definitely toxic to Tubifex, the lethal effects of the tap water of New Orleans are readily explained: This water is treated with ammonium salts to insure the retention of active chlorine at a minimum concentration of 0.7 parts per million. Stone's ability to keep Tubifex alive in the tap water of Philadelphia and of Columbia, Missouri, can be explained by the fact that these waters contain active chlorine at concentrations well below the lethal level.

Our results with various ions may partially explain the capricious distribution of Tubifex. In those stations from which we have collected Tubifex the phosphate concentration did not exceed 0.0002 molar. The pH ranged from 6.2 to 7.1. These conditions agree with those which we have found support the life of Tubifex in the laboratory in media made from distilled water, redistilled over sodium thiosulfate.

The diminution of the toxicity of the ions of ammonium sulfate by those of diluted amphibian Ringer's solution indicates the usual physiological interplay of ions.

It is interesting to note that the toxicity of phosphate ion was not significantly diminished by the presence of the ions of diluted amphibian Ringer's solution. Possibly the explanation of the toxicity of this ion lies in its reaction with calcium in the cutis of the worms. The explanation gains validity when it is remembered that the toxicity is enhanced by an increase in alkalinity. The toxicity of active chlorine is likewise not diminished by the presence of the ions of Ringer's solution.

The fact that active chlorine is toxic stands out as a token of the extreme sensitiveness of the worms to environmental factors, and suggests appreciable permeability of the cutis. It is in sharp contrast, furthermore, to our observations (unpublished) that the penetration of glucose and of glycine through the cutis of Tubifex is very slight.

Tubifex has become the subject of much quantitative study, and it is hoped that the data presented in this paper will obviate some of the difficulties which might arise in attempts to keep it alive in the laboratory.

According to Anderson and Zipkin ('39) ordinary distilled water prepared from strongly chlorinated tap water contains concentrations of active chlorine sufficiently high to influence analytical results. It is possible that such concentrations in a presumably innocuous sample of distilled water might modify significantly the responses not only of intact animals but even of tissue slices.

## SUMMARY

It has been shown that Tubifex is highly sensitive to the presence of active chlorine in any of its forms in concentrations above 0.6 parts per million (0.0000085 molar).

Tubifex is also a sensitive test object for studying the toxicity of single ions. It is killed by phosphate ion, the lethal concentration being lower at higher pH.

Ammonium ion is lethal to Tubifex in concentrations as low as 20 parts per million (0.0014 molar as ammonium ion). The toxicity is diminished by the presence of other ions.

The utility of Tubifex as a pharmacological test object is distinctly limited by its sensitivity to certain ions.

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## A PHOTOGRAPHIC TRANSECT FOR DETERMINING SOIL-COVER INDEX OF VEGETATION [1]

Technicians concerned with developing plant cover to control erosion need a convenient and reliable method of measuring the soil-protective value of vegetation, for use in evaluating, recording, and reporting progress in their work. The effectiveness of erosion-control demonstrations depends in part on the educational use made of the work accomplished. For this purpose a means is needed of making concrete comparisons of the erosion-control values of the cover on different sites, or on the same sites at different times.

For use by field men, whose principal responsibility is establishing vegetation rather than studying it by standard research methods, a satisfactory method must be one which is rapid, which requires a minimum of field equipment, and which yields definite quantitative values that can be duplicated by other workers under the same conditions. To be effective in education, it must provide a graphic record of results understandable to people not familiar with scientific methods.

In seeking a measurable criterion of erosion-control effectiveness, one finds little aid in the usual type of erosion investigations. Much has been done to determine the effect of different kinds of plant cover upon the rate of soil and water loss, but little attention has been given to measuring or analyzing the soil cover itself.

While these experiments show, for example, that Bermuda grass is a better erosion-control cover than corn, they show only by implication what qualities in a vegetative cover make it effective for this purpose and to what extent these qualities must be present to become effective.

Certain ecological investigations, however, indicate rather clearly that effectiveness in controlling erosion depends primarily upon the completeness of the layer of plant cover, living or dead, interposed between the soil surface and the agent of erosion (water or wind), rather than upon its composition, thickness, viability, or other characters, except as these affect its continuity.

Kramer and Weaver [2] showed that the parts of plants above the surface of the soil play a much greater part in preventing erosion than do the subterranean parts, and concluded that "prevention of erosion does not result so much from vertical thickness of cover as from one widely spread and continuous." These conclusions are confirmed by other studies.

Dodge [3] found a definite tendency for run-off to vary inversely with plant-cover density in

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[1] Credit is given Richard W. Hufnagle, Photographer, Soil Conservation Service, for guidance on many of the technical points of photography involved in this method.

[2] **Kramer, J., and J. E. Weaver.** 1936. Relative efficiency of roots and tops of plants in protecting the soil from erosion. *Neb. Univ. Cons. Dept. Bull. 12.* Lincoln, Neb. 94 pp., illus.

[3] **Dodge, A. F.** 1935. Measurement of run-off as influenced by plant cover density. *Iowa State Coll. Jour. Sci.* **9**: 399–407.

southern Iowa, and Larsen[4] reports similar results in a study of natural revegetation of eroded soils in southeastern Ohio. Aikman[5] found that within the vascular-plant stages of the secondary xerosere on an abandoned field in Iowa the amount of plant cover and the depth of soil profile increased with the advancing steps of succession.

In the West, the U. S. Forest Service has shown erosion and water losses to be correlated with range conditions as measured by standard range-survey methods (Forsling,[6] Bailey and Connaughton[7]). While range surveys do not take into account the litter on the ground, nor give equal value to all species of plants, since the purpose is to determine annual forage production rather than the protective value of the cover at any given time, such surveys do express roughly the density of the vegetation.

It seems evident, therefore, that the most important quality governing the erosion-control effectiveness of a given unit of cover is the completeness with which it covers the soil surface. This is the quality to be measured as an index to erosion-control value. In this function the dead plant parts may be as valuable as the living, and must be given their proportionate weight in the index.

Various methods have been used for measuring the density of plant cover, notably list, chart, and basal quadrats, tristats or photographic quadrats, line and belt transects (Weaver and Clements[8]), and range survey methods of which the square-foot-density method is standard (Stewart and Hutchings[9]). For the field worker in soil conservation, however, these usually are too laborious and require too much equipment to be carried in the field

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[4] **Larsen, J. A.** 1935. Natural revegetation on eroded soils in Southeastern Ohio. *Iowa State Coll. Jour. Sci.* **9**: 365–377.

[5] **Aikman, J. M.** 1935. The relation of the stages of plant succession to soil erosion. *Iowa State Coll. Jour. Sci.* **9**: 379–389.

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to be practical, or are unsatisfactory because they do not take into account all the cover (*i.e.*, litter, annual weeds, etc.) which functions in erosion control. Finally, the results are not easily understood by the layman.

In present practice the nearest approach to a satisfactory method of recording and showing the development of erosion-control cover is the use of photographs, which effectively record the general aspect of the site, and prove especially convincing if a "progress series" portraying conditions before treatment and at various stages during or after treatment is made. However, photographs afford no measure of the cover which can be expressed in numerical values for objective comparison. Moreover, the general aspect of a scene frequently does not express true conditions of soil cover. In photographs taken under some light conditions, the contrast between certain sorts of vegetation and the soil is not sufficient to show whether the soil is well protected or relatively barren.

To meet these deficiencies, the writer has experimented with a method which, for want of a better name, is referred to as the "photographic transect." Since he is one of the "field men" referred to above, whose duties do not leave opportunity for time-consuming research, the tentative technique is described here in order that others may test it in their work and more quickly establish its values or shortcomings.

The method is an adaptation of the tristat or photographic quadrat. It consists of inserting a white ruler between the cover and the soil and photographing it from such a distance that the figures on the ruler (or those portions which show through the vegetation) can be read on the prints. It is then possible to calculate on each print the percentage of the ruler which is obscured by the cover and to use this value to express the degree of protection afforded the soil. A similar technique, though somewhat differently applied, has been used by Wight,[10] p. 106 to measure the concealment afforded wildlife by vegetation.

For comparable results, a standardized procedure in using the photographic transect method is advisable. A white folding carpenter's rule 6 feet long has been found satisfactory for all conditions so far dealt with. It is inserted between the cover and the soil surface with as little disturbance as possible to either living or dead vegetation. In low herbaceous cover a 3-foot section is used; in coarser vegetation, the full length. The limits of the section of the ruler to be used in the calculations are marked by stakes in order that accurate measurements may be made in the

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Fig. 1. Photographic transect prints showing improvement of cover within gullied area fenced out of pasture. (A) General view; transect A located 4 yd. to right of flag on fence, transect B 3 yd. to left. (B) Vertical view of transect A, index 15. (C) Vertical view of transect B, index 44. (D) Horizontal view of transect A, index 57. (E) Horizontal view of transect B, index 80. Average index for transect A is 36, for transect B is 62.

photographs. At each location, the ruler is photographed from both "horizontal" and "vertical" viewpoints, being turned with each change in camera position so that the flat surface of the ruler faces directly into the camera lens.

For the "horizontal" view the camera is set up at a height of 1 to 2 feet from the ground and at a distance from the ruler which will permit the inclusion of the length to be photographed. Using a standard 9 × 12 cm. plate camera, the writer has found 6 feet distant and 1 foot high to be a practical position for photographing a 3-foot section of the ruler, and 12 feet distant and 2 feet high for a 6-foot section in coarser vegetation. The vegetation is cleared from in front of the camera to a distance from the ruler equal to the average height of the vegetation, and the camera is focused on the ruler, or, if this is not visible, on the stakes marking its position.

For the "vertical" view, the camera is set up on an ordinary tripod with a tilting top directly over the ruler, including as much of the length of the ruler as possible in the picture. None of the vegetation is removed for this photograph.

Since the ruler in each picture establishes the scale, it is not necessary to take great care always to locate the camera exactly the same distance from the sample, and no bulky equipment for this purpose is necessary. Several transects may be quickly located and photographed in an area, the locations marked by white flags, and a general photograph of the area made to show the distribution of the samples. The resulting series of pictures is an easily comprehended record of conditions.

By direct reading of the ruler, or by measurement on the print, the percentage of the ruler *obscured by cover of whatever sort* is calculated for each print. The average of the percentages obtained from the two photographs of each transect are used as the final soil-cover index for that particular sample of vegetation. These numerical values can be compared objectively and seem to express truthfully the relative amount and quality of erosion-control cover. Moreover, even persons who know nothing of quadrats or transects, and to whom the concept of "frequency-index" or other measures of plant density are entirely foreign, looking at the photographs can grasp quickly the idea of "measuring" vegetation by the familiar ruler, and can see for themselves the difference between sparse and dense cover.

It will be noted that the photographic transect secures only small samples of the cover for evaluation, which would be a disadvantage in accurate research work unless a correspondingly large number of samples were taken. How-

ever, for pictorial representation of conditions this is not especially serious since the fairness of the representation can be judged by the locations of the samples shown in the general view, and by the details of the cover visible alongside the ruler in each of the prints. Some error may be introduced also by the distortion of the images of stems and leaves near the lens with the result that they cover proportionately more of the ruler than they should. Whether this affects the values more than the chance location of the transect, or other variables in the method which may be expected to cancel one another, remains yet to be determined. The displacement of small plants and pieces of litter in inserting the ruler under low and sparse cover may also affect the values obtained. This will be true, however, only when the cover is too scant to prevent erosion, and utility of the method to show when an adequate cover has been secured will not be affected.

One example will serve to illustrate how the photographic transect method reveals differences in soil cover. A gully in a badly overgrazed pasture in Boone County, Nebraska, was fenced in the summer of 1934 to exclude livestock. In December, 1938, photographic transects were located on opposite sides of the fence to compare cover conditions (figure 1). The data recorded are shown in table I. The soil-

TABLE I. *Photographic Transect Data*

|  | Transect A Outside Fence | Transect B Inside Fence |
|---|---|---|
| Dominants | *Chenopodium* sp. *Ambrosia* sp. | *Rhus glabra* *Agropyron smithii* |
| Erosion | Active sheet | Not apparent |
| Horizontal index | 57 | 80 |
| Vertical index | 15 | 44 |
| Soil-cover index (average) | 36 | 62 |

cover indices here, as at other stations where the method has been used, seem truthfully to express cover conditions as appraised by general inspection.

It is hoped that the photographic transect method may be tested by other workers who are in a position to take enough samples for statistical evaluation, and under a wide variety of conditions where the results can be compared with measurements made by standard research methods to determine their reliability.

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## Mortality of Fishes Due to Cold on the Southeast Florida Coast, 1940

Observations reported by Storey and Gudger (1936) indicated that extraordinary depressions in temperature in South Florida may have severe effects on certain marine fishes. Since their data referred, however, only to the Sanibel Island and Tampa areas on the west coast of Florida, the following observations recently collected on the southeast coast from Miami to Key West seem worth recording. This latter area lies fifty to 100 miles farther south than the former.

First-hand observations were made by the writer at Miami and Key Largo; reports from reliable fishermen were taken for the Key Largo-Key West portion of the area. Thanks are due especially to Mr. Charles Brookfield and Mr. Claude Lowe for reports submitted. Good agreement existed among all reports. The area includes the Florida Key inlets and "creeks," Florida Bay, and Biscayne Bay—all of which lie in a region of shallow water ranging for the most part from one to four fathoms in depth. Since water temperatures were not available over the whole area, air temperatures and effects on vegetation are herewith noted as being indicative of the degree of the cold.

The period of killing cold came from January 27th to January 29th. Air temperatures were recorded as follows:

|             | Minimum | Mean   | "Normal" mean | Date      |
| ----------- | ------- | ------ | ------------- | --------- |
| Miami.....  | 36° F.  | 42° F. | 66° F.        | Jan. 27th |
|             | 31° F.  | 42° F. | 66° F.        | Jan. 28th |
| Elliott Key | 38° F.  | —      | —             | Jan. 28th |
| Key West.   | 50° F.  | —      | —             | Jan. 27th |

For the whole month of January, 1940, the mean temperature was 61° F., the lowest monthly mean on record with the Weather Bureau (records since 1896). Water temperature at Coconut Grove Docks on January 29th, 5 P.M., near ebb tide, was 51° F.; at Jewfish Creek near Key Largo, January 30th, 3 P.M. at high tide close to shore it was 55.4° F. Readings were not available for middle Biscayne Bay nor for Florida Bay. It is likely that these figures for water temperature do not represent the lowest points reached since they were taken after at least ten hours of insolation following the break in the cold period. The severity of the cold was indicated on land by noticeable damage to the following native trees: key mahogany, royal palm, coconut palm, guava, red mangrove, *Lysiloma*. Introduced tropical plants were, of course, severely injured or killed outright.

The following fishes were observed to be stunned or killed, and estimates were attempted as to relative numbers affected. The common names used by reporting fishermen are repeated here. Although these names have a rather consistent application in this area and are an indication at least of the general types affected, there were in some reports instances of failure to differentiate among several possible species as, for example, in the parrotfish and grunt groups. The terminology of Breder's (1929) Field Book of Marine Fishes was followed.

bonefish—*Albula vulpes* (L.)—many

moonfish—*Vomer setapinnis* (Mitchill)—many

mutton snappers—*Lutianus analis* (Cuvier & Valenciennes)—many

Lane snappers—*Lutianus synagris* (L.) (?)—many

grey snappers—*Lutianus griseus* (L.)—many

grunts—*Haemulon* sp.—many

porgies—*Calamus* sp.—many

mullet—*Mugil curema* Cuvier & Valenciennes—many

blue runners—*Caranx crysos* (Mitchill) ?—many

parrotfish—(species not differentiated in reports)—some

trunkfish—*Lactophrys* sp.—some

swellfish—*Spheroides* sp.—some

needlefish—*Strongylura* sp.—some

grouper—(species not determined)—a few

filefish—*Stephanolepis hispidus* (L.)—a few

brim—*Archosargus unimaculatus* (Bloch)—a few

barracuda—*Sphyraena* sp.—a few (small)

jack—*Caranx* sp.—a few

It is obvious that this list may have been prejudiced by reports of fishermen who were interested in collecting only the stunned specimens having some food or commercial value. That there were great numbers of these available is indicated by the estimate that nearly a million pounds of stunned but good specimens were sold during the period by fishermen from Key Largo to Key West.

These observations tend to confirm the general conclusions suggested by Storey and Gudger, namely, that rather rapid lowering of temperatures cannot be tolerated by many fishes in the shallow waters adjacent to the coast of South Florida, and that chilling, not gill-blocking with sediment, is the real factor leading to

death. In the recording here of water temperatures a beginning approximation is indicated for one tolerance-limit of some fishes of the area.

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## The Running Oak (*Quercus pumila* Walter)

It is recognized by botanists that, in general, the oaks may be arranged in two groups, depending upon whether their acorns mature the first autumn or the second autumn from flowering. Those maturing their acorns in the autumn of the first year from the opening of the flower belong to the white oak group; those maturing their acorns at the end of the second autumn are considered to fall in the black oak group.

While a few of the western black oaks mature their acorns the first autumn after flowering, our eastern white and black oaks have generally been considered separable on the basis of annual or biennial development of the acorns from the flower. As a matter of fact, all botanical keys dealing with our eastern oaks separate the black oak members from the white oaks on this basis. It would appear, however, that the Running Oak of the Eastern Coastal Plain is an annual fruiting black oak. For this reason an attempt was made to determine if the length-of-day factor was involved in this behavior.

Acorns of this oak collected by the late Mr. W. M. Lunn of the Division of Tobacco and Plant Nutrition, near Florence, South Carolina, in the Coastal Plain section, were received in 1933 and sowed in September. They germinated in a few weeks and were grown in large pails (fig. 1) and transferred to a series of length-of-day tests, the daily light periods ranging from 10 hours to the full length of day, by differences of one hour in the most instances.

Since this oak is a southern species and not particularly cold resistant, it was found necessary to protect the plants from low temperatures during the winter, either by keeping them dormant in a cold greenhouse of 50 to 55° F., or by keeping them in a closed unheated shed out of doors after the leaves had fallen in autumn. The young trees were given the same length-of-day exposures each following season, the tests starting in early spring, as soon as danger of heavy frost was over.

Trees began flowering on all the tests for the first time in 1936, two years from the germination of the acorns. At this time they were mere bushes, around 18 to 20 inches in height. Pollen appeared in late March, followed by a rapid development of the young acorns by mid-May. Those which remained were mature and falling in early September.

This annual fruiting behavior has remained the striking feature of these oaks for each sea-



FIG. 1. Plants of *Quercus pumila* growing since autumn, 1933, receiving full length of day during the summer at Washington, D. C.; kept in a large unheated darkened house from November to March. Height from 1.5 to 2.0 feet; acorns produced in abundance. (Photographed September, 1939.)

FIG. 2. Branch of a plant grown with full length of day, showing mature acorns developed in the current year. About three-fifths natural size. (Photographed September, 1939.)

son up to the present time, 1939, and for the most part, acorns have been produced in abundance (fig. 2). There is, however, no observable difference in flowering or in the maturity of the acorns for any season, whether the daily light exposure has been 10, 12, 13, or 14 hours, or the full length of day, which in June is near 15 hours in the latitude of Washington, D. C.

One point which deserves some mention is the fact that some of the leading floras treating the eastern oaks, have included this annual fruiting black oak in those sections of their keys which specifically refer to the acorns as biennial. Small in his *Manual of the Southeastern Flora*, has done so, and he also makes no mention of any annual fruiting behavior for this species.

William Trelease in his monograph *The American Oaks* characterizes the section Laurifoliae as having biennial fruit. In his description of the species *pumila*, however, he states that this oak is exceptional among the black oaks of the Atlantic region in the annual maturation of its fruit.

The ease with which this little oak can be grown in small containers if protected from severe winter conditions, and the promptness of flowering and fruiting at an early age under these conditions, suggest a number of problems. Since production of acorns from flowers at the end of the first summer seems to be so exceptional for our eastern black oaks, it would be of interest to learn if this annual fruiting black oak will hybridize with the various white oaks which also normally fruit the same season from flowering, since in the field the black and white oak members appear to hybridize more readily within their own groups. It would also be of interest to know if an annual fruiting black oak will cross with biennial fruiting species such as *Quercus cinerea;* and it would be of interest to know the affinities of this oak to its taller relative *Quercus cinerea* of the same geographical range. In these studies chromosome number would perhaps afford some information.

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## FOREST SERVICE RANGE RESEARCH SEMINAR

During the period July 10 to 22, 1939 a seminar on range research methods and procedures was held by the Forest Service, United States Department of Agriculture, at the Great Basin Experiment Station near Ephraim, Utah—a branch of the Intermountain Forest and Range

Experiment Station, with headquarters at Ogden, Utah.

Washington Office representatives of the divisions of range research, range management, and wildlife management, the directors, division leaders, and range research staff members of

the western regional forest and range experiment stations, the assistant regional foresters in charge of wildlife and range management of the western forest regions, and several other Forest Service members were in attendance.

This was the second meeting of this type to be held at the Great Basin Station during the last 10-year period. In 1931, an ecological and range methodology meeting was held under the auspices of the Ecological Society of America. Ecologists throughout the West participated.

The purpose of the 1939 intrabureau meeting was to aid in strengthening the Forest Service attack upon the broad western range problems and to redefine or clarify the objectives of the range research organization. Discussion centered around the problems being encountered, the methods to be used in their solution, and the other measures necessary to facilitate the conduct of range research and the dissemination of results.

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At the time of the 1939 meeting, range research had to its credit such contributions as the development of rotation-deferred system of grazing, invention and development of range reconnaissance or range surveys, foundation data on growth requirements and value of range plants, improved methods for grazing sheep and goats such as open and quiet herding and bedding them down in a new place every night, improved salting and better-placed watering places, the eradication of tall larkspur, the building of indicators of range conditions, and the crusading against range deterioration and erosion. These are contributions to management of the western ranges. But ahead are many complex problems such as the determination of the grazing capacity of western range types, proper degree and season of use for many of the key forage species, standards of range forage utilization, methods of artificial range revegetation, and improved methods of securing livestock distribution on the range. Inadequate information on these and closely related problems such as the correction of nutritional deficiencies of range livestock, plant breeding as an approach to forage improvement, interrelationships of rodents and other wildlife with range livestock, and the social and economic aspects of range livestock management hinders the most efficient use of the range forage resources.

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Solution of the many problems will require refinement of approach and improved experimental efficiency. Carefully drawn regional range problem analyses and carefully formulated working or study plans for individual experiments will assist in achieving the needed

refinement of approach. Greater efficiency in range studies will be promoted by improved experimental design and the use of statistical methods in analysis of data. However, use of such methods should be viewed as a means to an end, not the end in itself. Many of the more common experimental designs are suitable for use in range research, but in view of the gross nature of many of the measurement methods used in range experiments, new and more refined designs should be thoroughly reviewed before being extensively used.

Completion of studies concerned with the growth of the plant itself under range conditions, its ecological requirements, why it grows where it does and what facilitates its retention on the range, its normal development during the growing season and under grazing use, the relation of its growth to viscissitudes of climate, the relationships of its root and top growth, and its reproductive processes should provide valuable clues to the solution of more general problems of range management.

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But such studies of individual plants provide only a small fraction of the needed information. Since native vegetation, *in situ*, exists as a community whose constituents, either belonging to the same or to other species, are in constant competition with their neighbors, studies of the individual plant must be extended to investigations of the plant community. Such inquiries should deal with the undisturbed community as it reacts to climate and site, as well as with the manner in which such reactions are influenced by concurrent grazing use.

Information from such basic plant studies, logically combined with that derived from a comprehensive attack upon the problems of the interrelationships of grazing management, climate, and trends in plant/succession was envisioned as the logical approach to management of native range lands. Character of the plant community occupying an area and the vigor of its various constituents was viewed as providing a reliable record from which the character of past use may be judged and the type of future practices recommended—in other words, a comprehensive knowledge of plant succession would provide standards for judging range conditions.

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In measuring plants for tracing trends in vegetation, establishing range condition, measuring the forage crop, or for determining the degree to which forage plants have been harvested by grazing animals, there is a pressing need for critical evaluation of existing methods and for the development of new methods where existent ones are found to be inadequate.

Clipping of vegetation definitely has a place

in the solution of some specific range problems, especially for exploratory experiments in forage utilization. Results from clipping studies should be tested thoroughly on experimental ranges.

Enclosures, both temporary and permanent, are an indispensable tool for use in range studies, either in evaluating range use, or in studying the various factors related to management and other influences. One of their most important functions, for which more extensive use was urged, is to preserve remnants of native vegetation undisturbed. For any use the area enclosed should be fairly large.

Natural revegetation, through management, of low-value depleted range lands is the proper recourse in most areas. However, with many potentially valuable range lands, or critical watershed areas, artificial revegetation offers a promising and indispensable method of rehabilitation. But lack of specific information on species adaptability, methods of planting, relationship of site factors to growth requirements of suitable species, and plant selection and breeding retards more widespread use of reseeding.

Problems in handling livestock in experimental pastures, animal nutrition and its place in management of native ranges, dissemination of information derived by range research, and the recruiting and training of permanent personnel were other topics explored at the meeting.

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The responsibility of range research does not end with the solution of specific problems. Synthesis of data from the fields of plant ecology, plant physiology, soils, meteorology, animal husbandry, agronomy, and range economics into workable policies for fully integrated management of range and other wild land uses is the goal of range research. In accomplishing this goal the importance of cooperation and correlation of effort with all agencies concerned with range research and range land use was emphasized.

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## THE SOCIETY FOR THE STUDY OF SPECIATION

A society of individuals interested in various aspects of the dynamics of the origin of species is in the process of being organized. The members include Botanists, Zoologists, Bacteriologists and Anthropologists from the fields of Cytology, Genetics, Ecology, Paleontology, Physical Anthropology, Comparative Psychology, Taxonomy, Physiology, Embryology and the Biology of Populations.

It is not desired that one more formal organization be added to the large number of societies already in existence, but the need is felt for an informal cooperative group of scientists willing to pass information from one to the other. It is proposed that a rather informal information service be instituted through the publication of a booklet to contain recent bibliographies, information from the various laboratories and critical discussion of recent phases of the study of speciation. The dynamics of the origin of races and subspecies is included as a center of interest as well as the origin of higher categories which contribute to our knowledge of the origin of species.

No dues are contemplated at the present time during the period of organization, but a modest amount will probably be contributed by the members when the need and value of such an organization is manifest. The cost of organization and the first booklets is being defrayed through an anonymous grant.

The following men have agreed to act as an executive committee for the receipt of funds and the determination of policy: Edgar Anderson, John M. Beal, William Burrows, L. J. Cole, L. R. Dice, Th. Dobzhansky, Alfred Emerson (Secretary), A. C. Kinsey, W. M. Krogman, Raymond Pearl, Karl P. Schmidt, George G. Simpson, and Sewall Wright.

About 300 members have already joined the Society. Those interested are asked to communicate with the secretary.

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# TREE GROWTH BESIDE A RAIN GAUGE AND THERMOMETER

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This study of growth rate in trees as it is affected by temperature and precipitation is a continuation of efforts to analyze the essential relations between climate and forest trees in New England. In work previously reported (Lyon, '36, Goldthwait and Lyon, '37), the rates of secondary growth in Eastern Hemlock and White Pine were shown to be influenced by the water supply in the soil, provided by the generous but variable rainfall. Specifically, facts were offered to demonstrate positive correlations between width of annual ring and the rainfall of periods with unfrozen soil particularly in certain years marked by prolonged drouth or by a water supply well above the average. Perfect correlations between growth and the recorded precipitation of any one period of the year have not been found, partly because the water supply for the soil may be provided in different ways and at different times, although the rainfall of the growing season appears to be the most important single factor for Hemlock and White Pine.

There have been weaknesses in most of the work thus far reported. There is the primary difficulty of analysis of relations when so many factors of climate, soil, and nutrition of the tree act simultaneously to control the rate of secondary growth. Some students of tree physiology claim it is hopeless to expect control of growth by any one factor; everyone recognizes the complexity of the situation. Any results obtained as evidence for the importance of certain factors are bound to be affected by others; if any one

factor stands out it will be in spite of the others, and the evidence should be weighed accordingly.

With so many species of forest trees in the New England area, it is pertinent to ask why one or two should be selected for analysis of control by climate. It will certainly be necessary to measure the responses of several types of trees and wood before general statements can be framed. A start is being made in this analysis of six species on one site.

The most serious objection to conclusions drawn from work with tree-ring data and weather records has been lack of proof that temperatures and precipitation at the forest sites bear any close or constant relation to the conditions recorded by the instruments at some other site. Few opportunities have been found to take measurements of growth rate close to a station with a long series of weather records except for limited studies with increment borers. The data for this study are unquestionably comparable, but some evidence indicates that it is unnecessary to have the weather station so close to the trees, because the predominant climatic effects are much alike over a considerable area in northern New England.

## Methods and Materials

The hurricane of September, 1938, felled a mixed stand of trees in the College Park at Hanover, New Hampshire. The dominant trees were 70–80 years old, rooted in shallow soils over and beside a ledge with irregular outcrops. It was

fortunate and important for the study that most of the trees had been set out by hand and were all so evenly scattered over an area of 5 to 6 acres as to remove the possibility of distribution by soil and exposure preference for the species. The trees used for measurements of rings were selected for large numbers of rings and for freedom from unusual growth conditions for the area. They came from all the benches and slopes and from exposures that varied from north through east to south.

At the western edge of the site and at the same altitude (603 ft.) as the highest part of it, the records of rainfall have been taken continuously since 1862 and of temperatures since 1876. The data were furnished as monthly amounts of precipitation and monthly means of temperature by Prof. R. H. Goddard of the Shattuck Observatory at Dartmouth College. The basis for temperature was the daily mean, calculated as one-half the sum of the maximum and minimum. The deviations in the mean temperature of any one month were calculated from the station mean for 64 years. The station means for precipitation were based on the records for 78 years.

Six species of trees were measured in sufficient numbers to use for study. They included the native White Pine (*Pinus strobus* L.) and Red Oak (*Quercus borealis* Michx.) and the introduced Austrian Pine (*P. nigra* var. *austriaca* Schneid.), Scotch Pine (*P. sylvestris* L.), Norway Spruce (*Picea excelsa* Link.) and European Larch (*Larix decidua* Mill.).

The widths of annual rings were obtained from trunk sections cut at stump height and carried to the laboratory. The measurements were made according to the technique previously described (Lyon, '36 and '39), using a 10 × power binocular microscope and an ocular scale read in units of 0.1 mm. Each section was measured along three radii, and from 5 to 10 trees were used for each species. The use of three measurements for each ring

in a section not only provides a reliable index of the growth rate but also guarantees the accuracy of the date assigned to each ring, since the absence of a ring along one radius or a mechanical error in making measurements will be corrected along another radius.

### GROWTH RECORDS FROM THE RING MEASUREMENTS

The measurements for each tree section were recorded on printed forms which included a column each for the average width and the year of growth. Year for year, these average widths of ring did not vary much among the trees of the same species, since the fast growing trees and the slow growing trees had been eliminated as much as possible in the field selection. From one year to another, however, each tree varied greatly although some species showed more sensitivity in this respect than others.

Before using the ring measurements of any one section, attention was given to the years in which pronouncedly narrow or wide rings were formed. When the measurements for one tree were at variance in this matter of "cross identification" with other trees in the group, the tree was considered to be a poor indicator of growing conditions at the site. On this basis, a total of six sections, all of slow growing trees, were found to have growth rate sequences so unlike those in other trees of the same species that the records of their ring widths were set aside as too questionable for use.

The mean annual growth rates for the several kinds of trees in the study were obtained from the other trunk sections as follows: White Pine, 9 trees; Austrian Pine, 8 trees; Scotch Pine, 5 trees; Norway Spruce, 9 trees; European Larch, 10 trees; Red Oak, 6 trees. Only the average ring widths for these groups of trees are reported and used in this study. They are shown by the six line graphs in figure 1, all plotted to the same scale from base lines indicated for them. They

show: (1) the greater vigor of growth in early years of a group of essentially even-aged trees of most species; (2) the differences in growth rates among the species represented. The data are used in this study, however, for an analysis of relations between the annual growth increments of the species and of the possible control of secondary growth rate by climatic factors.
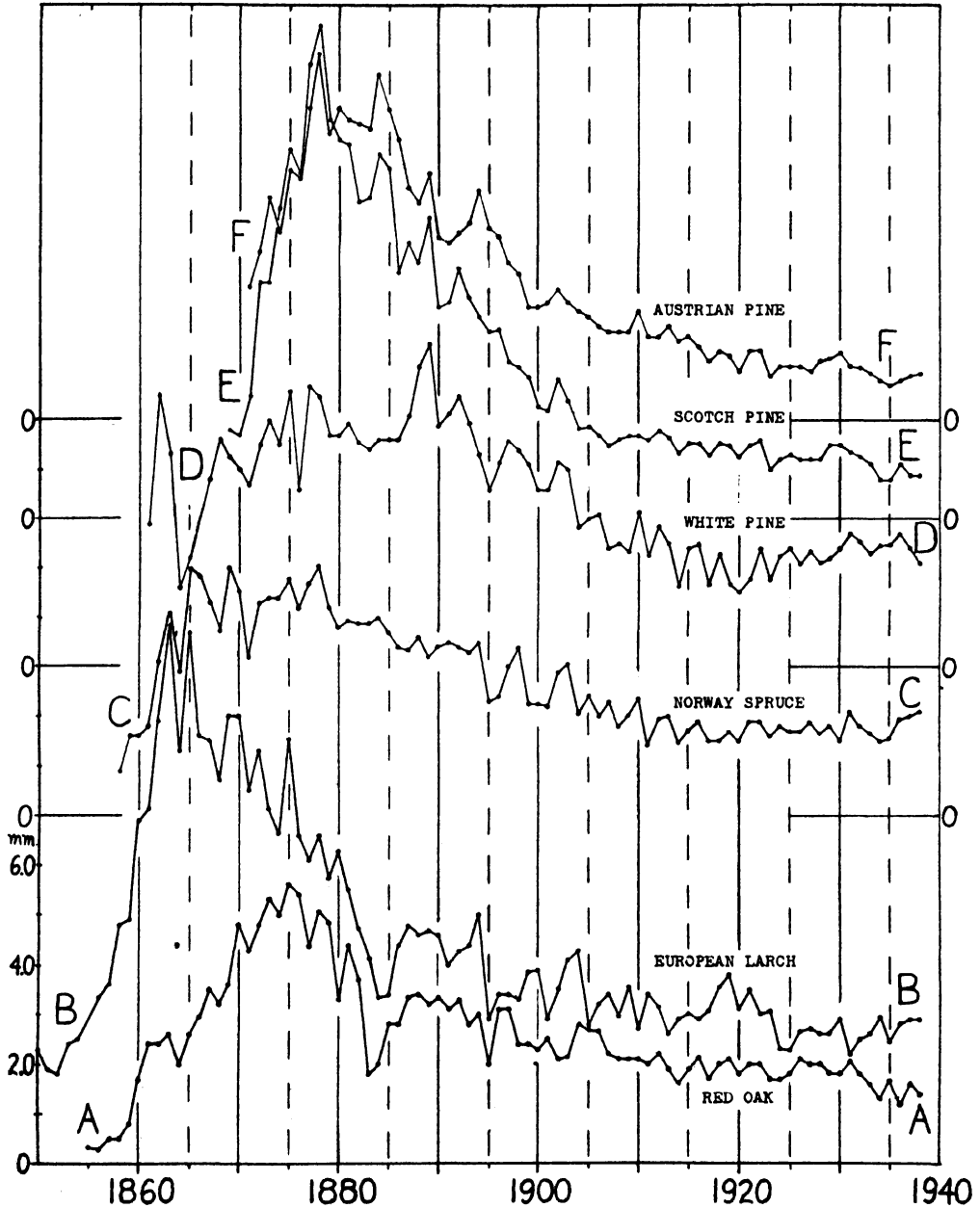


FIG. 1. Increments of secondary growth in 6 species of trees, grown in a mixed stand. Mean ring widths on vertical axis with supplementary base lines for graphs C–F that are plotted on same scale as A and B. Each graph represents mean radial growth increments, measured from several trees for each species as follows: A, 6 trees; B, 10 trees; C, 9 trees; D, 9 trees; E, 5 trees; F, 8 trees.

## DISCUSSION AND ANALYSIS OF DATA

Inspection of the tables and graphs of ring widths showed that the variations in the mean growth rates from year to year were not wholly fortuitous but indicative of rather consistently low or high growth rates in certain years. Since most of these years were known for other reasons to have been marked by drouths or generous water supply respectively, the six species were regarded as presumably sensitive to climatic changes that affect water supply. The data for each species were accordingly subjected to statistical analysis of their growth increments year by year, in relation to each other and to the records of rainfall and temperatures. The study of interrelations between the species was particularly important because no record of such an analysis could be found in the literature.

It is evident from the graphs in figure 1 that absolute values for the growth rates of any species depend so much upon age and vigor that the variations due to cli-

matic factors must be calculated from a trend or standardizing line (Douglass, '36, Schumacher and Meyer, '37). Such a trend line was therefore drawn for the data of each species and tested carefully for the balance of plus and minus departures of the annual increments from the trend for the group in any calendar year. Two of these trend lines are shown in figures 2 and 3. For all six of these curves of reference, sometimes considered as normal curves of growth, the ring widths were plotted on a scale that permitted a reliable estimate to 0.01 mm. in the annual departure from the trend or normal for a given year.

The extent to which the six species responded alike to their environment was measured by means of standard correlation coefficients ($r$), calculated from the departures for each year according to the formula

$$r = \frac{\Sigma xy}{\sqrt{\Sigma x^2 \cdot \Sigma y^2}},$$
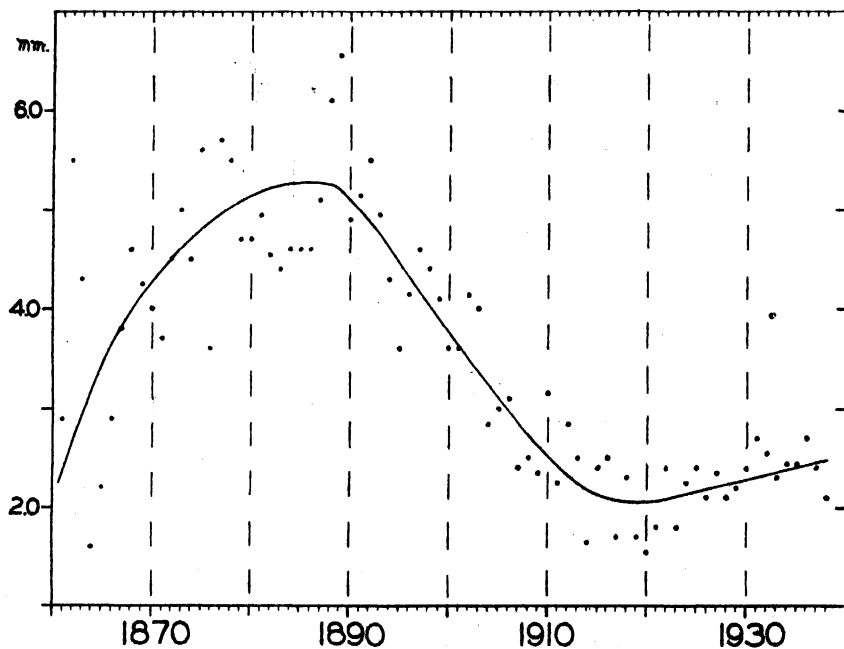


FIG. 2. Trend line for radial increments of secondary growth in White Pine. Data shown by dots, each representing a mean of measurements from 9 trees. See fig. 1, $D$ for line graph of same data.
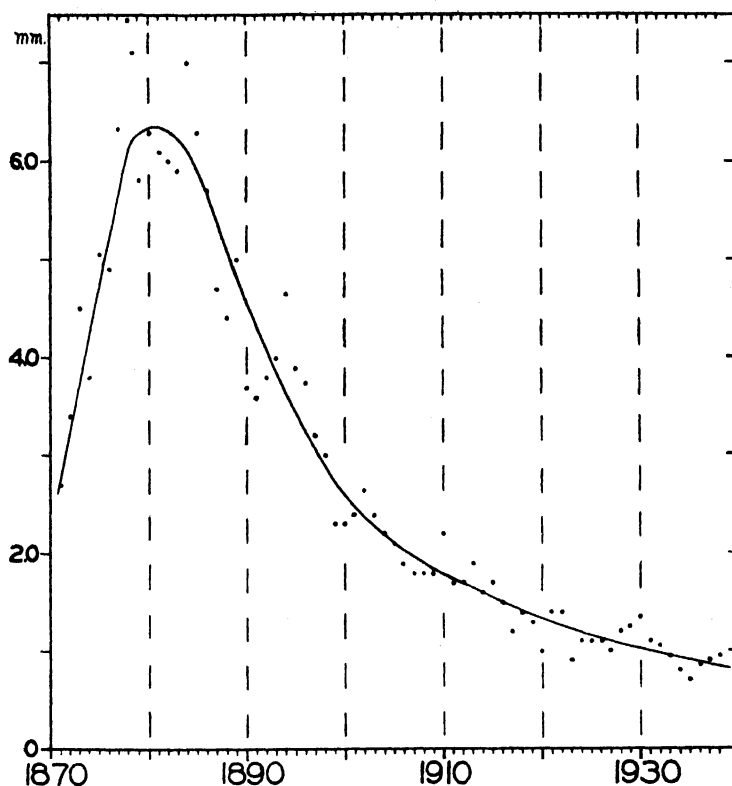
Fig. 3. Trend line for radial increments of secondary growth in Austrian Pine. Data shown by dots, each representing a mean of measurements from 8 trees. See fig. 1, F for line graph of same data.

where $x$ and $y$ are the departures of the two variants from their respective means or normals. Following the usage of Fisher concerning the significance of values obtained, each calculated $r$ was referred to Fisher's table (as printed by Snedecor, '37, page 125) and the degree of significance noted. The nature of the correlations in the annual growth rates of

the six species appears in table I, where the symbol 0 stands for not significant, + for significant and ++ for highly significant.

The table shows the excellent agreement among the evergreen pines and spruce and between the two deciduous species. The immediate inference can be drawn that the primary control of growth rate

TABLE I. *Nature of correlations in the annual growth rates of the six species*

|  | White Pine | Scotch Pine | Aust. Pine | Spruce | Larch | Oak |
|---|---|---|---|---|---|---|
| White Pine |  | ++ | 0 | + | ++ | ++ |
| Scotch Pine | ++ |  | ++ | ++ | 0 | 0 |
| Austrian Pine | 0 | ++ |  | + | 0 | 0 |
| Norway Spruce | + | ++ | + |  | ++ | 0 |
| Europ. Larch | ++ | 0 | 0 | ++ |  | ++ |
| Red Oak | ++ | 0 | 0 | 0 | ++ |  |

Key to symbols: 0 indicates not significant.
+ indicates positive and significant.
++ indicates positive and highly significant.

lies outside the individual trees, since the variations in their crowns, root systems, nutrition and other contributing factors are overshadowed by common environmental influences. Of the evergreens, White Pine alone gave a strong correlation with both Oak and Larch, perhaps because the "critical" years, with some environmental factor causing a wide departure from trend in these species, outweigh statistically the many other years with variable response between the two types of trees.

Further analysis of the interrelations in the growth rates of the six species would require year by year comparison of the data plotted in figure 1. This is done later in connection with rainfall notes, but it is sufficient to notice here that in the many critical years of dependence upon some single factor or like combination of factors at least five of the six species respond alike to the change in environment from the preceding year. The two species that usually provide one dissenter for the year are Oak and Larch, as we should expect from the table of correlations (table I).

\* \* \*

The analysis of relations between rainfall and annual growth rates was guided in part by previous experience with pine and hemlock trees in humid New England. In this study the comparisons were to be made quantitatively by the method of correlation coefficients just outlined, using for the trees the plus and minus departures from trend or normal for the

species at the site, and for the rainfall the corresponding annual departures from the arithmetical, 78-year mean of the station.

The other two new factors in the work were the variable responses of the six species and the decision to include the data for all years rather than limit the analysis to the "critical" years with shortage or abundance of what seemed to be water supply. However, both these points only meant more calculations for months and groups of months that gave promise of positive or negative correlations between growth rates and amounts of precipitation. These periods were tentatively determined by inspection and simple tabulations of agreement between the plus and minus signs for each pair of figures, year by year. Most of the preliminary tests indicated lack of correlation, shown by an even balance between sign agreement and non-agreement, as the laws of chance provide. No further mention will be made of these unproductive tests but they were made of such periods as the calendar year, the water year (October to October) of water companies, the September to September period, and the March and April periods, just before tree growth starts.

Table II gives in summary form all the significant correlations that appeared between growth rates and precipitation. The correlations are all positive and the symbols 0, + and + + are used to indicate the nature of each.

The apparent response of the White Pine to rainfall is the outstanding point

TABLE II. *Nature of correlations between the growth rates of the species and the rainfall record*

| Rainfall of | White Pine | Scotch Pine | Aust. Pine | Norway Spruce | Europ. Larch | Red Oak |
|---|---|---|---|---|---|---|
| 1. June | + + | + | 0 | 0 | 0 | 0 |
| 2. May–July | + + | 0 | 0 | 0 | 0 | + |
| 3. April–July | + + | 0 | 0 | 0 | 0 | + |
| 4. April–August | + + | + + | 0 | 0 | 0 | + |
| 5. Apr.–Aug. plus preceding Sept.–Nov. | + + | + | 0 | 0 | 0 | 0 |
| 6. Apr.–July plus preceding Sept.–Nov. | + + | 0 | 0 | 0 | 0 | + |

Symbols used as in table I.

shown by this series of correlation studies. The species is clearly very sensitive to the water supply of its growing season, more so than claimed by previous workers with it (Brown, '15, Burns, '29, Goldthwait and Lyon, '37). The highly significant coefficients for all six of the periods is surprising; comparison of them shows the highest value (.545 ± .055) for the April–August period while June gives the lowest (.343 ± .069) but this is still well above the 1 per cent level (.292 for the number of degrees of freedom in the computation).

Scotch Pine and Red Oak were the only other species to correlate with rainfall records but the value of $r$ was always less than the smallest for White Pine. Scotch Pine gave indication of dependence upon summer as well as spring rains while the Oak showed more effect of water supplied between April 1 and August 1. Very little carryover from the fall rains (September–November of preceding year) appeared for these species, although White Pine had shown some response to them.

In the absence of any other practical method for measuring the extent of agreement between growth rates and rainfall of stated periods, a year by year comparison was made between them for each species. The results of this comprehensive survey are given in table III. An entry was made in the body of table III for a particular year and species only when the signs of growth rate departure from the trend and of rainfall departure from the arithmetical mean were alike. The table is therefore a statement of positive correlations, year by year, between the relative growth rates of each species and the precipitation of certain periods of the year. These periods are the same as those that appeared in table II.

In addition to the columns which show the positive correlations for each year covered by the growth records, the first column is used to indicate by a — or + sign the relative width of the rings in years marked by essentially like response

of the growth rates of at least 5 of the 6 species; the last column provides notes on the water supply for years in which it was far from the mean for certain periods or in which the nature of the growth response called attention to the probable conditions of soil moisture during the growing season.

In making the entries for agreement in sign between relative growth rate and relative rainfall for the six periods of table II, it was necessary to use key numbers for the different periods. It will be noted from the key that some of the periods overlap other periods but the positive correlations for most of the years could not have been indicated in the table by naming the months without making it too cumbersome to use easily. The series of numbers across the table for any one year makes a graphic demonstration of the agreement or lack of agreement in growth responses of the six species. Use of the word "average" in a few places indicates the absence of any growth rate departure for the year and species, because the trend line passed through the point plotted.

The positive correlations of table III are summarized in table IV. In this form the degree of dependence of the growth rate of each species upon the rainfall of the several periods of the year, is brought out better than in table III.

It is not easy to interpret these agreements between variations in growth rates and in rainfall quantities, with the mathematical signs of both determined with reference to the trend or mean. Some agreement must be attributed to chance, but this is offset by two important considerations—the masking effect of climatic factors other than rainfall, and the absence of data for the quantities of water that actually entered the soil in any period. The distribution of the precipitation over a monthly period is known to vary so greatly that a period may be recorded as abnormally wet when the water actually came late or early in the period or in such heavy rains that only a frac-

tion entered the soil. There is also the conflicting effect of temperature which may indirectly increase or decrease the water supply while it directly lowers or raises the growth rate of the meristematic tissues.

Taking the data as they stand, the relative growth rates of most years can be accounted for on the basis of water supplied by the rainfall of some period. The years with no agreement with precipitation data vary from 16 per cent for White

Pine to 29 per cent for Larch. For every species, the most common agreement by far was with all six of the rainfall periods; in many years (1871, 1880, 1882, 1883, 1886, 1895, 1900, 1922 and 1931) this held for at least five of the six species simultaneously. Calculated on the basis of all years in the record, this correlation with the six periods of the year amounted to 26 per cent for White Pine, 25 per cent for Red Oak and 23 per cent for Scotch Pine. If the need of agree-

TABLE III. *Agreement of growth rate departures from normal growth curves with the rainfall departures from 78-year mean*

Key    1 = June    2 = May–July    3 = April–July    4 = April–August
5 = Apr.–Aug. plus preceding Sept.–Nov.    6 = Apr.–July plus preceding Sept.–Nov.

| Ring | Year | White Pine | Scotch Pine | Aust. Pine | Norway Spruce | Larch | Red Oak | Notes |
|---|---|---|---|---|---|---|---|---|
| + | 1863 | 4 | | | 4 | 4 | 4 | Wet Aug. |
| − | 64 | 1–6 | | | 1–6 | 1–6 | 1–6 | Dry year |
| | 65 | 2–6 | No data | No data | | | 1–6 | |
| | 66 | 1–6 | | | | 1–6 | | |
| | 67 | 2, 3, 6 | | | 5 | 2, 3, 6 | 1, 4 | |
| | 68 | 1–4 | | | | | | |
| | 69 | 5, 6 | 5 | | 5 | 5, 6 | 2–4 | |
| | 1870 | 1–4 | 1–4 | | 5, 6 | 5, 6 | 5, 6 | Dry fall |
| − | 71 | 1–6 | 1–6 | No data | 1–6 | 1–6 | 1–6 | Dry year |
| | 72 | | 1–5 | | 6 | 1–5 | 6 | |
| | 73 | | 1–6 | | 1–6 | 1–6 | | |
| | 74 | | 2–6 | | | | | |
| + | 75 | 1, 2, 5 | 1, 2, 5 | 1, 2, 4, 5 | 1, 2, 4, 5 | 1, 2, 5 | 1, 2, 5 | Wet spring |
| | 76 | 2–6 | 1–6 | 2–6 | 2–6 | 1 | 1 | |
| | 77 | 2–5 | 1–6 | 2–6 | 1–6 | | | Wet year |
| + | 78 | 5, 6 | 5, 6 | 5, 6 | 5, 6 | 5, 6 | 5, 6 | Water store |
| | 79 | 2–6 | 2–6 | 2–6 | 1 | 2–6 | 1 | |
| − | 1880 | 1–6 | 1–6 | 1–6 | 1–6 | | 1–6 | Dry |
| | 81 | 3–6 | 3–6 | 3–6 | 3–6 | 1 | 2 | Dry |
| − | 82 | 1–6 | 1–6 | 1–6 | 1–6 | 1–6 | 1 | Dry |
| − | 83 | 1–6 | 1–6 | 1–6 | Average | 1–6 | 1–6 | Dry |
| | 84 | 1–6 | | | | 1–6 | 1–6 • | Dry |
| | 85 | 1, 2, 3, 5, 6 | | 4 | 4 | 1–3, 5, 6 | 1–3, 5, 6 | Dry |
| − | 86 | 1–6 | 1–6 | Average | 1–6 | 1–6 | 1–6 | Dry |
| | 87 | 1 | | 1 | 1 | 2–6 | 2–6 | |
| | 88 | 1, 4 | 2, 3, 5, 6 | 2, 3, 5, 6 | 1, 4 | 1, 4 | 1, 4 | Wet fall |
| + | 89 | 2, 5, 6 | 2, 5, 6 | 2, 5, 6 | 3, 4 | 2, 5, 6 | 2, 5, 6 | Wet spring |
| | 1890 | 1 | 1 | 1 | 2–6 | 2–6 | 2–6 | |
| | 91 | 5, 6 | 2–4 | 2–4 | 5, 6 | 2–4 | 5, 6 | Wet fall |
| + | 92 | 1–5 | 1–5 | 6 | 1–5 | 1–5 | 1–5 | Wet spring |
| + | 93 | 1, 2, 4 | 1, 2, 4 | 1, 2, 4 | 1, 2, 4 | 1, 2, 4 | 1, 2, 4 | Dry Apr. |
| | 94 | 1–6 | | | | | | Dry |
| − | 95 | 1–6 | 1–6 | | 1–6 | 1–6 | 1–6 | Dry |
| | 96 | 1–6 | | | 1–6 | 1–6 | | |
| + | 97 | 1–6 | 1–6 | 1–6 | 1–4 | | 1–6 | Wet |
| | 98 | 1 | 2–6 | 1 | 1 | 2–6 | 2–6 | Wet June |
| | 99 | | 2–6 | 2–5 | 2–5 | | 1–6 | |

TABLE III.—*Continued*

| Ring | Year | White Pine | Scotch Pine | Aust. Pine | Norway Spruce | Larch | Red Oak | Notes |
|---|---|---|---|---|---|---|---|---|
| — | 1900 | 1–6 | 1–6 | 1–6 | 1–6 |  | 1–6 | Dry |
| — | 01 | Average | 1 | 1 | 1 | 1 | 2–6 | Dry June |
| + | 02 | 2–4 | 2–4 | 2–4 | 1–4 | 1–6 |  | Moist |
| + | 03 | 1, 2, 5 | 1, 2, 5, 6 | 1, 2, 4–6 | 1, 2, 5 | 1, 2, 5, 6 | 3 | Dry Apr. |
|  | 04 | 1–6 | 1–6 |  | 1–6 |  |  |  |
|  | 05 |  |  |  | 1–6 |  | 1–6 |  |
|  | 06 | 2–6 |  |  |  |  | 2–6 |  |
|  | 07 | 2, 4, 5, 6 | 2, 4, 5, 6 | 2, 4, 5, 6 | 1, 3 | 1, 3 | 1, 3 |  |
| — | 08 | 1–4 | 1–4 | 1–4 | 1–4 | 1–4 |  | Dry |
|  | 09 | 1–6 |  | 1–6 |  |  |  |  |
| . | 1910 |  |  |  |  | 1–6 |  | Dry |
| — | 11 | 1, 5, 6 | 1 | 1, 5, 6 | 1, 5, 6 | 2–4 | 1, 5, 6 | No store |
| + | 12 | 5, 6 | 5, 6 | 3–6 | 5, 6 | 3–6 | 5, 6 | Water store |
|  | 13 |  |  |  |  | 1–6 | 1–6 | Dry |
| — | 14 | 1, 2, 3, 6 | 1–4, 6 | 3, 4 | 1–6 | 1–4, 6 | 1–4, 6 | Dry |
|  | 15 | 2–4 | 2–4 | 2–4 | 1, 5, 6 | 1, 5, 6 | 1, 5, 6 |  |
|  | 16 | 1–4 | 1–4 |  | 1–4 | 5, 6 | 1–4 | Spr. moist |
| — | 17 | 3, 5, 6 | 3, 5, 6 | 3, 5, 6 | 3, 5, 6 | 4 | 3, 5, 6 | No store |
|  | 18 | 1 | 1 | 1, 4 | 2, 3, 5, 6 |  | 1 |  |
|  | 19 | 1, 3, 4 | 5 | 1–4 | 5, 6 |  | 5 |  |
| — | 1920 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 3–6 | 1, 2 | Spr. dry |
|  | 21 | 1–6 |  |  |  |  |  | Fall wet |
| + | 22 | 1–6 | 1–6 | 1–6 | 1–6 | 1–6 | 1–6 | Spr. wet |
| — | 23 | 1, 4–6 | 1, 2, 4–6 | 1, 2, 4–6 | 1, 2, 4–6 | 3 | 1, 2, 4–6 | No store |
|  | 24 | 3–6 | 1, 2 | 1, 2 | 3–6 | 1, 2 | 1, 2 |  |
|  | 25 | 1–6 | 1–6 |  |  |  |  |  |
|  | 26 | 1–3 | 1–3 | 1–3 | 4 | 4–6 | 4–6 |  |
|  | 27 |  | 1–6 | 1–6 |  |  |  |  |
|  | 28 |  | 1, 2 | 1–6 |  | 1–6 | 1–6 |  |
|  | 29 | 1, 2, 4–6 | 3 | 3 | 2, 3 | 3 | 1, 2, 4–6 |  |
|  | 1930 |  |  |  | 1, 3–6 |  | 1–6 |  |
| + | 31 | 1–6 | 1–6 | 1–6 | 1–6 |  | 1–6 | Wet |
|  | 32 |  |  |  |  | 1–6 |  | Water store |
|  | 33 | 2 |  |  | 2 |  | 2 |  |
|  | 34 | 3, 6 | 2, 4, 5 | 2, 4, 5 | 2, 5 | 3, 6 | 2, 4, 5 |  |
|  | 35 | 1–6 |  |  |  |  | 1–6 |  |
|  | 36 | 4–6 | 4–6 | 3, 6 | 4, 5 | 4–6 | 1–3 | Wet fall |
|  | 37 |  |  | 1–6 | 1–6 | 1–6 | 1–6 | Wet spring |
|  | 1938 | 1, 3, 5, 6 | 1–3, 5, 6 | 4 | 4 | 4 | 4 | Wet Aug. |

ment with the single month of June be omitted, the percentage of positive correlations is increased appreciably for the pines and oak.

Complete proof that water supply is the dominant factor for growth control cannot be found in this series of comparisons alone, but the evidence is augmented considerably for its importance to White Pine, Scotch Pine, and Red Oak. Schwarz (1899) in Germany and Robbins ('21) in Missouri reported observa-

tions on Scotch Pine and Red Oak respectively, in general agreement with our evidence for these species. More recently Fuller ('38) in Illinois has reported for one tree of Red Oak a good agreement with rainfall of the calendar year.

\* \* \*

Another climatic factor that can be checked statistically with growth rates is temperature. The most logical measure of it is the daily mean temperature, and

TABLE IV. *Extent of agreement between growth rate and rainfall of stated periods*

|  | White Pine | Scotch Pine | Aust. Pine | Norway Spruce | Larch | Red Oak |
|---|---|---|---|---|---|---|
| Total no. of years | 76 | 70 | 66 | 76 | 76 | 76 |
| Years not agreeing | 12 | 16 | 18 | 17 | 22 | 16 |
| Years accounted for | 64 | 54 | 48 | 59 | 54 | 60 |
| Agreement with June | 42 yrs. | 35 yrs. | 26 yrs. | 35 yrs. | 32 yrs. | 39 yrs. |
| Agreement with May–July | 44 yrs. | 42 yrs. | 31 yrs. | 33 yrs. | 34 yrs. | 40 yrs. |
| Agreement with April–July | 42 yrs. | 35 yrs. | 28 yrs. | 32 yrs. | 35 yrs. | 33 yrs. |
| Agreement with April–Aug. | 42 yrs. | 35 yrs. | 32 yrs. | 37 yrs. | 36 yrs. | 37 yrs. |
| Agreement with S − N + Apr.–Aug. | 43 yrs. | 37 yrs. | 27 yrs. | 39 yrs. | 36 yrs. | 40 yrs. |
| Agreement with S − N + Apr.–July | 41 yrs. | 32 yrs. | 26 yrs. | 32 yrs. | 36 yrs. | 38 yrs. |
| Agreement with all six periods | 20 yrs. | 16 yrs. | 11 yrs. | 16 yrs. | 17 yrs. | 19 yrs. |
| Agreement with all but June | 4 yrs. | 4 yrs. | 3 yrs. | 2 yrs. | 2 yrs. | 5 yrs. |
| Agreement with all but fall ppt. | 4 yrs. | 3 yrs. | 2 yrs. | 4 yrs. | 1 yr. | 1 yr. |
| Agreement only with fall ppt. | 4 yrs. | 2 yrs. | 1 yr. | 5 yrs. | 4 yrs. | 4 yrs. |
| Agreement only with June ppt. | 4 yrs. | 4 yrs. | 4 yrs. | 4 yrs. | 3 yrs. | 4 yrs. |

reliable records of it beside the College Park trees were used in correlation studies of its relations to the growth rate.

The selection of months and groups of months with some promise of positive or negative correlations between growth and temperature was made on the basis of preliminary tests of agreement between the signs of departures from trend and mean respectively. This was the method already described for locating correlation between growth and .rainfall. In every case of doubt, a significant correlation was assumed possible and tested by a complete calculation. Most of the preliminary tests, for periods that need not be described in detail, proved a lack of correlation. Only those of special interest

are included in table V which also gives by symbols the significant correlations found, all positive with one exception.

Before noting the bearing of these results upon the question of growth control by temperature, it is necessary to set the probable time for start of secondary growth in the tree trunks. This is directly possible for only part of the species and then with some uncertainty, due to lack of information on the point. In Germany, Schwarz (1899) worked on the basis of May–August as the growing-season for Scotch Pine, and it should start no earlier in northern New England. From the work of Brown ('15) in New York, it is probable that White Pine does not start its secondary growth before

TABLE V. *Correlations between growth rate departures from trend, and departures of daily mean temperatures from 64-year mean*

|  | White Pine | Scotch Pine | Aust. Pine | Norway Spruce | Europ. Larch | Red Oak |
|---|---|---|---|---|---|---|
| January | 0 | 0 | 0 | 0 | 0 | 0 |
| February | 0 | 0 | 0 | 0 | 0 | 0 |
| March | ++ | 0 | + | ++ | + | 0 |
| April | ++ | + | ++ | + | 0 | 0 |
| March–April | ++ | + | ++ | ++ | + | 0 |
| May | 0 | 0 | 0 | − | + | 0 |
| June | 0 | 0 | 0 | 0 | 0 | 0 |
| July | 0 | 0 | 0 | 0 | 0 | + |
| May–July | 0 | 0 | 0 | 0 | 0 | 0 |

Key to symbols: 0 indicates not significant.
− indicates negative and significant.
+ indicates positive and significant.
++ indicates positive and highly significant.

May 1. Lodewick ('28) found only spring wood of Red Oak (*Quercus borealis* var. *maxima*) formed at Syracuse, New York, on June 2, 1920. From comparable work with *Quercus velutina* in 1923 by the same investigator, it is doubtful if growth begins before May 1 in our northern oaks, particularly at Hanover, New Hampshire, where the general growing season is shorter.

We have no information about the growth periods of the other conifers used in this study, but presumably they correspond roughly to that of White Pine or of *Thuya occidentalis* which Lodewick studied in 1920 and 1923. During 1920 he found in the latter "no evidence of xylem increment in late April"; from all his work he concluded (p. 35) "In this conifer, xylem production begins in late May or early June." Lodewick also followed the growing seasons of five other species, including maple, elm, and ash trees, without finding a case of wood formation at breast height before May 1.

In the absence of better information it therefore seems reasonable to consider the effects of temperature on tree growth in northern New England to be indirect before May, with the bare possibility that some pre-conditioning influence may occur. This undemonstrated effect might come through the nutritive processes of the foliage on the evergreen trees or through internal changes in the cambium of any species. With this possible effect in the background, it seems fair to assume, for this area, a growing season for each of the six species to start no earlier than May 1.

The noteworthy effects of temperature as shown in table V are those of early spring for the conifers and of July only for the Red Oak. The effects of March and April temperatures are equally great and always positive while in the two cases involving May temperatures, the correlation coefficient is negative for Norway Spruce and positive for European Larch.

Taking first the significant positive cor-

relations for March and April, there is one logical connection with the growth processes of the tree. The effect must be through the water supply to the soil about the roots or to the general water table. The melt waters of the winter's snow and the precipitation of March and sometimes part of April enter the soil if it is not frozen, or run off to the streams, depending primarily on the air temperatures of March and early April. The idea agrees well with experience in the area but is a new consideration for understanding climatic control of tree growth, although Schwarz (1899) noted the direct response of Scotch Pine in Germany to the temperatures of January–March. With a monthly mean temperature of 28.8° F. at Hanover, New Hampshire, March air is clearly so near the freezing point that plus departures will thaw the ground while minus departures may even add frost as the normal snow cover disappears. The facts reported by Schwarz agree perfectly with this interpretation although Schwarz seemed to favor a pre-conditioning effect for which he offered no evidence. The effect of April temperatures on the storage of water cannot be explained so readily, but the statistical analysis is acceptable proof of a positive influence on later growth. There is no other explanation so reasonable, although it is possible that the air temperature of April affects the soil temperature of early May by reason of the slow transmission of heat from the air into shaded forest soils.

In the course of the computations required for each correlation coefficient of temperature effects, it was frequently observed that for the years when no agreement appeared between rainfall and growth increment there was agreement of growth rate with March and April temperatures. If the indirect effect of temperature through water supply is accepted as proved, the unexplained years of table IV can be reduced in number as

follows:

> White Pine, from 12 to 5
> Scotch Pine, from 16 to 7
> Austrian Pine, from 18 to 11
> Norway Spruce, from 17 to 10
> European Larch, from 22 to 13
> Red Oak, from 16 to 11.

Further reduction might have been obtained if the temperature record had started before 1876, but the greatest discrepancy (for Austrian Pine and Larch) is now only 17 per cent of the total rings used in the analysis of relations between growth rate and water supplied.

The effects of May temperatures appear clearly for only two species. The negative coefficient for the Norway Spruce points strongly to the dependence of its growth increment upon the water in the soil during May, conserved by temperatures below the mean of 54.6° or lost by evaporation during the May days that average warmer than this mean temperature for the month. For European Larch, the positive coefficient suggests that much of the annual growth is made during May and that the optimum temperature for wood formation is considerably above the mean for May.

## CONCLUSIONS

A survey of all the correlations found for each of the six species may be summarized as follows: White Pine is very sensitive to the water supplied by rainfall of various periods and by the temperature of the early spring months. Scotch Pine is less sensitive to the supply of water, but its growth responds well to moisture supplied from April through August. Austrian Pine depends primarily upon the water provided prior to the growing season but a combination of factors is in control during the period of active growth. Norway Spruce grows in proportion to the water made available by temperature effects of the period March to May inclusive. European Larch profits from water supplied in early spring,

particularly by abnormally high March temperatures, but during May it also grows in direct proportion to the temperature of the air. Red Oak alone fails to show a significant correlation with water supplied before the growing season, but its growth does depend somewhat upon the rain that falls during its growing season. This species of oak was unique also in its significant growth response to July temperatures, a relationship that is not unexpected in view of the preference of oaks for warm climates.

Because this analysis was made from weather records and tree-ring measurements from the same small site, its accuracy should be high, but there is some question of the general validity of the conclusions for tree growth on other sites in the region when the rates of growth are to be predicted from the weather records of the infrequent stations. Certain evidence is available on the point for White Pine because the work reported by Goldthwait and Lyon ('37) was based on comparable measurements for this species, using trees cut at some distance from the weather records station. The critical point is the similarity in yearly growth rates between the trees they used and the trees of the same species that were analyzed in this study.

The relations between the growth of the two sets of trees have been estimated by correlation coefficients based on departures from the trend or normal curve in all cases. Pairing the Hanover trees of this study against each of the four lots of trees mentioned by Goldthwait and Lyon, the nature of the correlations was as follows:

Hanover vs. Norwich, Vt.—*highly significant*

Hanover vs. Hartland, Vt.—*highly significant*

Hanover vs. Enfield, N. H.—*significant*

Hanover vs. North Conway, N. H.—*significant.*

From these p o s i t i v e correlations, strongest for the trees that grew nearest

each other, it is probable that the White Pine that grew beside the weather records station made yearly growth responses to climate essentially the same as those of other trees growing as much as 65 miles away (North Conway, N. H.). Other evidence to establish this broad climatic effect upon tree growth as a general rule for trees sensitive to the water supply factor will be reported later.

## SUMMARY

Mature trees of six species that grew beside the weather records station at Hanover, New Hampshire, were used to compare their rates of secondary growth, and to seek relations between growth rate and the records of rainfall and temperature in a New England valley forest. After mean ring widths for each species were plotted against calendar years, a tested trend line for each permitted calculation of yearly deviations for periods of about 70 years each. Correlation coefficients were computed and found to be significant among most of the evergreen species and between the deciduous oak and larch. For the full length of their growth records, White Pine, Scotch Pine and Red Oak gave significant, positive correlation coefficients with the rainfall of certain periods of the year, but Austrian Pine, Norway Spruce and European Larch showed no consistent agreement with precipitation records when the growth increments of all years were considered.

The daily mean temperatures by months were compared with the annual growth rates in the same way. There was little agreement between growth increments and temperatures of the growing season, but all the coniferous species gave significant positive correlations between growth of the year and the temperatures of March and April, before the growth started. This effect of temperature is interpreted as indirect; it controls the growth in later months by determining the amount of water which the forest soil receives from melting snow and from the precipitation of March and April. A delayed effect of April air temperatures upon the soil temperature of early May is also possible.

With few exceptions, all the relations disclosed by this analysis emphasize the importance of water supply as a controlling factor of growth rate in northern trees. Specific conclusions are reached for the water supply relations of each species used in the study, but White Pine was outstanding for its sensitivity to the water made available to its roots.

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# THE ANNUAL ENERGY BUDGET OF AN INLAND LAKE[1]

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## INTRODUCTION

The variation in the quantity of solar radiation delivered to the surface of an inland lake during the course of the year is the principal factor in determining the physical, chemical and biological cycle of changes that take place within the water. This is true especially of lakes which are situated in temperate latitudes where there are considerable differences between summer and winter temperatures of the air and of the water.

In the deeper lakes which become covered with ice for a few to several weeks during the winter, the annual cycle consists of four phases which correspond roughly to the four seasons of the year. (1) There is a winter stagnation period in which the water is inversely stratified while the lake is covered with ice; that is, the warmest water is at the bottom and the coldest at the surface. (2) There is an overturning and circulation of the entire body of water following the disappearance of the ice in spring.

(3) As the temperature rises above the point of maximum density (4° C.) in the spring, the free circulation of the water is hindered as a result of the difference in density between the warm upper layer and the cold lower stratum; this is due to the fact that most of the warming takes place in a comparatively thin upper stratum. From 65 to 90 per cent or more of the sun and sky radiation is cut off by the upper meter of water, depending upon the color and the transparency. This large reduction is due chiefly to reflection at the surface, to the rapid absorption of the radiation by the water itself and by the stains and suspensoids that may be present in the water.

With the further rise in the temperature of the upper water as the season advances, a summer stratification is established. This is a direct stratification in which there is a warm upper stratum, a cold lower stratum and a transition zone between them in which the temperature changes rapidly from that of the warm upper water to that of the cold stratum below; naming them in order from surface to bottom, they are known as the epilimnion, the thermocline or mesolimnion, and the hypolimnion. In the deeper lakes these three strata persist throughout the summer.

(4) The fourth stage is represented by the autumnal cooling and overturning, which is followed by a complete circulation of the water until the lake becomes covered with ice.

The circulation of the water in spring and autumn distributes the dissolved substances uniformly from surface to bottom, but a more or less marked difference in the chemical character of the upper and lower strata develops during the two stratification periods, especially in summer.

The seasonal changes in the physical and chemical characteristics of the water have an important effect upon aquatic life. The spring rise in temperature speeds up life processes and the increase in the amount of solar radiation at this time makes conditions more favorable for photosynthesis. Likewise the circulation of the water in spring and autumn brings dissolved substances into the upper stratum, which is the zone of photosynthesis, where they can be readily obtained by the aquatic plants. The phytoplankton responds promptly to these favorable growing conditions and, as a result, the standing crop of plankton is usually much larger during the two circulation periods

[1] From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and reports No. 92.

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than it is at the time of summer and winter stratification.

The annual cycle of changes that is induced by the march of the seasons naturally raises the question of the amount of energy actually involved in the phenomenon as a whole and also in the various phases of the cycle. This problem is a very complex one and a large amount of data is necessary to evaluate each of the several items.

Limnological studies have been in progress on Lake Mendota at Madison, Wisconsin, for many years and the data accumulated in these investigations make it possible to give approximations of the quantity of energy involved in a number of the items. Quantitative studies of some of the factors have not been made up to the present time and a more complete assessment of the energy budget of the lake will have to await such investigations.

The annual energy budget of a lake may be regarded as comprising the energy received from sun and sky each year and the expenditures or uses which the lake makes of this annual income of radiation. In general the annual income and outgo substantially balance each other. This is true more particularly of the physical energy budget. Considerable biological material produced in one energy year lives over into the next, but this overlapping crop of organisms is much the same in quantity from year to year so that it plays approximately the same annual rôle. For this reason it does not require any special consideration. There is a certain amount of organic material contributed to the bottom deposits in the deeper water and to peat formation in the shallow water which lasts for long periods of time, but the annual energy value of these materials is so small in most cases that they may be neglected.

The minimum balance in the annual energy budget is found at the time the lake becomes covered with ice. The mean date of freezing of Lake Mendota is December 18 and this date may be taken as the close of one energy year and the beginning of the next. It thus closely approximates the calendar year.

## DATA

Lake Mendota has an area of 39.4 square kilometers, a maximum depth of 25 meters, a mean depth of 12.1 meters and a volume of 478,370,000 cubic meters (Juday '14).

The additional data that form the basis for the estimation of the annual energy budget relate chiefly to the physics and to the biology of the lake. Extended studies of the chemistry of the water have been made, but these may be disregarded in the general consideration of the energy budget. The decomposition of the organic matter, for example, affects the chemistry of the water by removing oxygen and adding carbon dioxide, but this oxidation produces a certain amount of heat which helps to warm the water and it thus appears in the physical budget. Likewise the metabolic activities of the living organisms give rise to some heat which also contributes to the warming of the water.

One of the most important factors in the assessment of the energy budget is a knowledge of the amount of solar and sky radiation actually delivered to the lake during the course of the year; such a record covering a period of 28 years is now available for Lake Mendota. The observations on the temperature of the water comprise several thousand readings covering a period of more than 20 years. These and other pertinent data make it possible to compute the annual heat budget of the water. In addition the annual heat exchanges of the bottom deposits have been investigated; the thickness of the ice has been measured for a number of years and the evaporation during the greater part of the year has been determined for a period of 6 years.

The biological investigations include a quantitative study of the plankton for more than 6 years, as well as quantitative

observations on the large aquatic plants of the shallow water and on the bottom animals at all depths. Also estimates of the annual yield of fish have been obtained.

The biochemical data consist of quantitative determinations of the organic nitrogen, nitrogen-free extract, crude fiber, organic carbon, and ether extract of the plankton material, of the large aquatic plants, of the bottom animals, and food analyses of the fish. From these analyses the amount of crude protein, carbohydrate and fat in the various organisms can be computed and their energy value thus roughly determined; these results give some idea of the rôle which the aquatic plants and animals play in the energy budget of the lake.

## PHYSICAL ENERGY BUDGET

*Amount of Solar Radiation.*—In April 1911, a pyrheliometer was installed on the roof of North Hall, University of Wisconsin, by the United States Weather Bureau for the purpose of measuring the amount of solar and sky radiation that reaches the surface of the earth in this region. A recording instrument has been kept in constant operation since that date, so that a 28 year record was completed in March 1939.

The instrument is located only a short distance from the south shore of Lake Mendota and the record, therefore, represents the amount of solar and sky radiation delivered to the surface of the lake

TABLE I. *Normal amount of radiation received from sun and sky on a horizontal surface at Madison, Wisconsin, during the different months of the year*

The results are stated in gram calories per square centimeter of surface and the records cover a period of 28 years, or from April 1911 to March 1939, inclusive.

| | | | |
|---|---|---|---|
| January | 4,639 | July | 16,392 |
| February | 6,406 | August | 13,986 |
| March | 9,881 | September | 10,186 |
| April | 11,940 | October | 7,217 |
| May | 14,695 | November | 4,385 |
| June | 15,577 | December | 3,568 |
| | | Entire year | 118,872 |

annually. The general results for the 28 year period are given in table I which shows the mean quantity of radiation for the different months of the year and also the annual mean. My thanks are due Mr. Eric R. Miller, Meteorologist of the Weather Bureau Station, for these data; he has been in charge of the recording apparatus since its installation in 1911.

In the following discussion, the energy unit is the gram calorie and the unit of area is the square centimeter. For the sake of brevity, the amounts of energy are indicated as "calories" in most cases instead of using the complete expression "gram calories per square centimeter of surface."

Table I shows that the monthly means of solar and sky radiation delivered to the surface of Lake Mendota during the 28 year period ranged from a minimum of 3,568 calories in December to a maximum of 16,392 calories in July. The annual means for the 28 years varied from a minimum of 108,597 calories in 1935 to a maximum of 129,659 calories in 1937. As indicated in the table, the annual mean for the 28 years is 118,872 calories.

*Melting of Ice.*—In early spring a considerable part of the solar radiation is utilized in melting the ice. The lake is covered with ice for a period of 12 to 16 weeks each winter and the average maximum thickness of the ice for 24 years between 1901 and 1930 was 48 centimeters. For a specific gravity of 0.92, a column of ice one square centimeter in area and 48 centimeters long weighs about 44 grams. Since it requires about 80 calories of heat to melt a gram of ice, it would take a little more than 3,500 calories per square centimeter of surface to remove the covering of ice each spring. A similar amount of energy is liberated when the water changes to ice in freezing, but no data have yet been obtained to show what happens to this energy that is given up in the freezing process. The 3,500 calories used in melting the ice constitute a little more than 35 per cent of

the mean quantity of radiation delivered to the surface of Lake Mendota during the month of March, when most of the melting of the ice takes place. An undetermined amount of energy is also utilized in melting the snow that may accumulate on the ice during the winter.

The mean date for the opening of the lake is April 5, but this event depends upon the character of the weather in March. If the weather is mild, the lake may become free of ice at any time during the last ten days of this month; if it is severe, however, the opening may be delayed until about the middle of April, or even later occasionally. For convenience in computation, April first may be taken as the opening date of the lake and the beginning of the spring and summer warming period.

*Heat Budget of Water.*—The annual heat budget has been defined as the amount of energy required to raise the temperature of the water from the mean winter minimum to the mean summer maximum. The lowest mean temperature of the water is found at the time the lake freezes over and the highest mean temperature is usually attained in August. A certain amount of this warming takes place in winter, or between the time of freezing and the last of March, but by far the larger part of the rise in temperature is found during the April-August warming period.

The mean temperature of the water of Lake Mendota is about 1° C. at the time of freezing and 2.5° when the ice disappears in spring; this represents an average increase of 1.5°, which gives a winter heat budget of about 1,800 calories. This result is obtained by multiplying the mean increase in the temperature of the water (1.5°) by the mean depth of the lake (1210 centimeters). The main contribution to the winter heat budget comes from the solar radiation that penetrates the ice, especially in late February and in March. Some 500 calories are derived from the heat stored in the lake bottom during the summer, while an undetermined amount

comes from the inflowing water of streams and springs, and from the internal heat of the earth.

After the disappearance of the ice, a large part of the solar and sky radiation is utilized in warming the water. In general the spring and summer warming period may be regarded as extending from April 1 to August 31, but there is little or no gain in heat after the middle of August. During this warming period 72,-500 calories of radiation are delivered to the surface of the lake (table I). The temperature of the water rises from a mean of 2.5° at the time the ice disappears to a maximum mean of 21° in August, a net increase of 18.5° during this period. This gives a spring and summer heat budget of 22,400 calories, which is about 31 per cent of the total radiation delivered to the surface of the lake during the April-August warming period.

Adding the winter heat budget of 1,800 calories to the spring and summer heat budget of 22,400 calories gives an annual heat budget of 24,200 calories; this amounts to about 20 per cent of the total quantity of radiation delivered to Lake Mendota during the course of the year. This annual heat budget does not represent a strikingly large amount of energy when stated on the unit area basis, but it gives a much more impressive result when applied to the total volume of water in the lake; computations show that it would require the combustion of about 1,350,000 tons of anthracite coal to warm the entire body of water from its mean winter minimum to its mean summer maximum temperature.

*Heat Budget of Bottom.*—

depth of 5 meters. More than 200 sets of bottom temperature readings were taken between 1917 and 1920. Four different stations were used and the depths of the water ranged from 8 meters at the shallowest to 23.5 meters at the deepest one.

The results showed that the annual heat exchange at the 8 meter station was about 3,000 gram calories per square centimeter, while that at the deepest station was 1,100 calories, with intermediate amounts at the other two stations. For the entire lake bottom, the mean annual heat budget was a little more than 2,000 calories. About a quarter of the heat which the water gains in winter while the lake is covered with ice comes from that which is stored in the bottom during the spring and summer.

*Evaporation.*—Another important factor in the physical energy budget of Lake Mendota is the loss of heat due to evaporation. Ralph ('13) reported the results of a quantitative study of evaporation made by Professor L. S. Smith, College of Engineering, University of Wisconsin. The evaporating pan used for the experiments was placed in a small creek flowing into the lake in order to avoid difficulty from waves, so that the readings probably represent maximum results for the lake itself. The observations covered the various months from April to November, inclusive, between 1906 and 1911. The number of monthly records during the 6 years ranged from three in November to six in August and September. The November observations extended only to the tenth of the month in one year, to the eighteenth in another and to the eighteenth in a third when they had to be discontinued on account of freezing weather.

The results are obtained, however, serve as a basis for the computation of the evaporation for the month of November been used for the estimation of the December evaporation.

The mean quantity of various months, as for the period in which

TABLE II. *The mean amount of evaporation in the different months during 1906 to 1911, inclusive*

The results are expressed in inches and in centimeters. The December evaporation is estimated on the basis of the November rate; it extends to December 18, the mean date of freezing.

| Month | Number of years | Mean evaporation | |
|---|---|---|---|
| | | Inches | Centimeters |
| April....... | 4 | 2.24 | 5.69 |
| May....... | 4 | 2.98 | 7.57 |
| June....... | 4 | 2.92 | 7.42 |
| July........ | 5 | 2.89 | 7.34 |
| August..... | 6 | 2.59 | 6.58 |
| September.. | 6 | 2.05 | 5.21 |
| October.... | 5 | 1.94 | 4.93 |
| November.. | 3 | 1.27 | 3.23 |
| December... | 0 | 0.76 | 1.93 |
| Total...... | | 19.64 | 49.90 |

the lake is not covered with ice. The average temperature of the surface water is 2.5° on April 1, rises to a maximum of 24.2° in July and then falls to a mean of about 1° at the time of freezing in December. The mean of the weekly averages from April to December is 14.7°, but a mean of 15° is used for the computation of the heat losses due to evaporation. The heat of vaporization of water at 15° is a little more than 587 calories per gram.

The average evaporation during the April–December period amounted to 49.9 centimeters (table II) which may be taken as 50 centimeters annually for purposes of computation; this amount represents approximately 50 grams of water per square centimeter of surface, and

TABLE III. *Quantity of solar and sky radiation used by Lake Mendota in various physical and biological processes*

The results are indicated in gram calories per square centimeter of surface.

Melting of ice in spring . . . . . . . . . . . . . . . 3,500
Annual heat budget of water . . . . . . . . . . 24,200
Annual heat budget of bottom . . . . . . . . . 2,000
Energy lost by evaporation . . . . . . . . . . . 29,300
Annual surface loss . . . . . . . . . . . . . . . . . . 28,500
Loss by conduction, convection and radiation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 30,324
Biological energy budget (maximum) . . . . 1,048

the vaporization of this quantity of water requires a little more than 29,300 gram calories.

The respective amounts of energy included in the four items of the physical energy budget which have been considered so far are indicated in table III. The sum of these four items is 71,000 calories, which is approximately 60 per cent of the mean quantity of energy delivered to the surface of Lake Mendota annually by sun and sky.

*Seasonal Changes in Energy Budget.—* An analysis of the seasonal components of the energy budget will give a better idea of what happens to some of the energy that is not included in the four items discussed above.

*Winter.—*The quantity of radiation delivered to the surface of Lake Mendota between December 18, the mean date of freezing, and April 1, the approximate date of opening, is 22,400 calories (table I). Only a small percentage of this radiation, however, contributes directly to the energy budget of the lake. The entire winter heat budget of the water is 1,800 calories and some 500 calories of this amount come from the bottom deposits where it is stored during the summer. This leaves 1,300 calories to be derived directly from the winter radiation and from the inflowing water of streams and springs that may be warmer than the water of the lake. While no data have yet been obtained regarding the amount of heat contributed by spring and stream waters, it is probably so small in quantity that it may be disregarded. Thus the 1,300 calories in the winter heat budget of the water represent less than 6 per cent of the radiation that reaches the lake during the winter.

In February and March each year, however, about 3,500 calories are utilized in melting the covering of ice, so that the total winter utilization of radiation by the lake is 4,800 calories, which is about 21 per cent of the amount delivered to the surface during this season; this gives a winter loss of 17,600 calories of

radiation that do not play any part in the energetics of the lake. Apparently the covering of snow and ice is very effective in cutting off the radiation during the winter. Part of the radiation is reflected and part of it is absorbed by the snow and ice.

*Spring and Summer.—*In the spring and summer warming period, a certain amount of radiation is reflected from the surface and another portion is scattered back out of the water by particles in suspension. The amount reflected depends upon the condition of the sky, the surface of the water, the season of the year and the time of day. In the course of a clear day in mid-summer, the quantity of radiation reflected varies from about two per cent when the sun is near the zenith to 100 per cent when it is at the horizon.

Results obtained by Davis ('40) with a continuous recorder and Weston Photronic cells showed that the surface loss for an average clear day in July was 5.2 per cent of the total amount of radiation delivered to the lake during the day. Changes in the sky and in the water conditions may increase this surface loss and there is an increased loss from reflection in early spring and late summer owing to the lower altitude of the sun. On the basis of these variations, it seems safe to assume that the surface loss for the entire warming period (April 1 to August 31) is 10 per cent of the energy delivered to the lake during this time. The total available energy for this period is 72,590 calories (table I) and 10 per cent of this amount may be taken as 7,300 calories. The summer heat budget o- the water is 22,400 calories and the lent from evaporation (34.6 centimeter The water from April to August, inclls to is about 20,300 calories; these tv lake is plus the surface loss of 7,30ature of amount to 50,000 cories, w¹he largest about 22,590 calories of there found in summer energy income of er and winter counted for.

No data have been o complexities, it

will show just how this quantity of energy is lost; conduction, convection and radiation are involved in the problem, but the relative importance of the three factors has not been ascertained. The losses due to these factors would be largest during the early part of the warming period when the temperature of the air at night and on cool, cloudy days falls below that of the water. Similar but less pronounced losses take place during the summer; undoubtedly there is some loss of heat at night during the entire summer, with the possible exception of the warmest parts of July and August. The daily fluctuations in temperature in spring and summer have not been studied up to the present time; it is a complex problem and continuous records with self-registering instruments would have to be made for a considerable period of time in order to secure data for its solution.

*Autumn.*—The autumn cooling period (September 1 to December 18) offers another complex problem for the analysis of the various energy losses. During this time the temperature of the water falls from the highest to the lowest mean of the year. The autumn losses of heat come from three different sources, namely, (1) the annual heat budget of the water (24,200 calories), (2) a large part of the heat stored in the bottom in the spring and summer warming season and (3) the heat accumulated by the water in the autumn from direct insolation.

The quantity of radiation delivered to the lake in the autumn is approximately 24,000 calories. Since the sun is at a lower altitude at this season, the surface ɔss of energy from reflection will be ʌɲewhat larger than in summer and it *of i.* be taken as about 15 per cent, or Th square calories. This leaves 20,400 calo- a perioɔenetrate the water and take part 1939, incˑrgy budget. To this extent di- January...ˑon playɤa rôle in determining February...ˑʟoling of the water. Evapo- March....... April........ this period is about 15.3 May......... lʌle II), which accounts June......... 15,ˑʌt 9,000 calories; thus

reflection and evaporation together represent 12,600 calories, or a little more than 52 per cent of the autumnal radiation delivered to the lake, leaving a balance of 11,400 calories in the autumnal energy budget which is lost by conduction, convection and radiation.

*Surface Losses.*—These analyses of seasonal energy changes show that the surface losses due to reflection and upward scattering amount to about 17,600 calories in winter, 7,300 calories in spring and summer, and 3,600 calories in autumn; this is a total of 28,500 calories, or 24 per cent of the annual radiation delivered to the lake. This surface loss added to the first four items in table III amounts to 87,500 calories, or 74 per cent of the solar and sky energy reaching the lake each year. The remainder, 31,372 calories, constitutes the losses due to conduction, convection and radiation in the physical energy budget and it also includes the small amount of energy represented in the biological energy budget. In round numbers some 22,000 calories received by the lake during the spring and summer warming period are lost by conduction, convection and radiation, while 9,000 calories received during the autumn cooling season are lost in a similar manner. This leaves only 372 calories for the biological energy budget, but the amount may be as great as 977 calories as shown in the discussion of the biological energy budget in the next section, or 1,048 calories including the dissolved organic matter. •

BIOLOGICAL ENERGY BUDGET

A certain amount of the solar radiation that passes into the water of Lake Mendota is utilized by the aquatic plants in the process of photosynthesis. The products of this assimilation, namely, proteins, fats and carbohydrates, thus constitute the primary accumulation or storage of the energy derived from the sub-surface illumination. Since this organic material manufactured by the plants serves, either

directly or indirectly, as a source of food for all of the non-chlorophyllaceous organisms that inhabit the lake, these latter forms, therefore, constitute a secondary stage in the storage of the energy accumulated by the aquatic plants. The original amount of energy represented by these secondary organisms varies with the different forms, depending upon the number of links in their respective food chains; in general they represent a comparatively small proportion of the primary organic material manufactured by the plants.

Chemical analyses of the various aquatic organisms have now progressed far enough to enable one to compute their energy- values from the standards that have been established by food chemists. The standard values are 5,650 calories per gram of protein, 9,450 calories per gram of fat and 4,100 calories per gram of carbohydrate, on a dry weight basis. These values do not represent the total quantity of energy utilized by the aquatic organisms, however, because a part of the synthesized material is oxidized in the metabolic processes of the living organisms. These metabolic oxidations result in the production of heat which is transmitted to the water, but the quantity of heat derived from this source is extremely small in comparison with that which comes from direct insolation.

The amount of organic matter consumed in the metabolism of plants is much smaller than that in animals because several grams of plant material may be consumed in the production of one gram of animal tissue even in animals that feed directly on plants; the predaceous animals represent a still larger quantity of the original photosynthesized material.

*Plankton.*—A quantitative and chemical study of the plankton of Lake Mendota was made by Birge and Juday ('22) during a period of more than six years. The plankton studies also included a quantitative determination of the bacterial flora by Fred, Wilson and Davenport

('24) using the plate method and by Bere ('33) using the direct count method. The bacterial component of the plankton, however, was found to be comparatively small; it amounted to 5 milligrams of dry organic matter per cubic meter of water as compared with 1,974 milligrams in the total plankton.

The studies of Birge and Juday showed that the average standing crop of plankton amounted to 240 kilograms of dry organic matter per hectare of surface. The range was from a minimum of 141 kilograms in February to a maximum of 287 kilograms per hectare in December. The annual production of plankton, however, can only be estimated. This is due to the fact that so many complexities are involved in the problem. The plankton is made up of a wide variety of organisms which differ greatly in size and in rate of reproduction; also both production and destruction of the constituent organisms go on continuously throughout the year, without any break whatever to indicate the end of one crop and the beginning of another.

The rate of turnover in the plankton crop depends chiefly upon the rate of reproduction of the various organisms and the reproductive rate, in turn, is affected by temperature, radiation and other physical factors, as well as by chemical and biological agencies. Under favorable conditions, the bacteria may divide several times during the course of a day and the algae may double or quadruple their numbers daily. On the other hand, the rotifers and crustacea may require one to several weeks to go through a complete life cycle, but these slow reproducing forms make up only about 6 per cent of the total quantity of plankton. The rate of reproduction of all forms falls to a minimum in winter when the lake is covered with ice and the temperature of the water is 2° C. or less. The largest standing crops of plankton were found in spring and fall, with summer and winter minima.

In view of all of these complexities, it

may be estimated that the average turn-over in the organic matter of the mean standing crop of plankton takes place about every two weeks throughout the year. It would be more frequent than this in spring and summer, and less frequent in winter. A turnover of 26 times per year would give an annual yield of 6,240 kilograms of dry organic matter per hectare of surface as indicated in table IV. This material would consist of

TABLE IV. *Annual production of plankton, bottom flora, bottom fauna and fish, as well as crude protein, ether extract (fat), and carbohydrate constituents of the organic matter*

The results are stated in kilograms per hectare on a dry, ash-free basis. The plankton yield is based on a turnover every two weeks during the year. The average quantity of dissolved organic matter is included also.

|  | Dry organic matter | Crude protein | Ether extract | Carbo-hydrate |
|---|---|---|---|---|
| Total plankton..... | 6240 | 2704 | 431 | 3105 |
| Phytoplankton... | 5850 | 2501 | 383 | 2966 |
| Zooplankton..... | 390 | 203 | 48 | 139 |
| Bottom flora...... | 512 | 64 | 6 | 442 |
| Bottom fauna...... | 45 | 33 | 4 | 8 |
| Fish............. | 5 | 3.4 | 1 | 0.6 |
| Dissolved organic matter.......... | 1523 | 334 | 68 | 1121 |
| Total organic matter | 8325 | 3138.4 | 510 | 4676.6 |

2,704 kilograms of protein, 431 kilograms of fat and 3,105 kilograms of carbohydrate. Approximately 94 per cent of the organic matter comes from the phytoplankton and 6 per cent from the zooplankton.

*Bottom Flora.*—A quantitative study of the large aquatic plants of Lake Mendota was made by Rickett ('22). These plants are limited to areas where the depth of the water does not exceed 8 meters. From the shoreline out to this depth, the annual crop of large aquatics amounted to 2,000 kilograms per hectare, dry weight. If evenly distributed over the entire lake, this crop would give a yield of 628 kilograms per hectare. A little more than 18 per cent of this material consisted of ash, so that the organic

matter was equivalent to 512 kilograms per hectare.

Schuette and some of his students (1922–29) made chemical analyses of certain species of these plants and several others have been analyzed in more recent years, so that the energy values of all of the more common forms can now be computed from the data in hand. The results of such computations are given in table IV. The 512 kilograms of dry organic matter per hectare consisted of 64 kilograms of protein, 6 kilograms of ether extract or fat and 442 kilograms of carbohydrate.

The bottom deposits, especially in the deeper water, contain a rather large population of bacteria. Williams and McCoy ('35) and Henrici and McCoy ('38) found half a million up to four million bacteria per cubic centimeter of mud in the upper few centimeters of the deposits in the deeper water, but there were only about one-tenth as many at the shallow water stations. While these organisms are present in considerable numbers, they are so small in size that they add very little to the crop of organic matter in the lake; so they have been disregarded. Likewise fungi are fairly abundant in the bottom deposits, but no quantitative study of them has yet been made; it seems probable that their contribution to the organic content of the lake is negligible from an energy standpoint.

*Bottom Fauna.*—Muttkowski ('18) made a quantitative study of the bottom fauna of the shallower water, or from the shoreline out to a depth of 7 meters. While his results were given only in number of individuals per unit area of bottom, average weights of the various forms were subsequently obtained so that the weight of the material could be computed. Chemical analyses of some of the forms were made at the time of his investigations and others were made later; from these analyses the energy values of the shallow water bottom fauna have been computed.

The bottom fauna of the deeper water

was studied by Juday ('22); this investigation included numerical, gravimetric and chemical results. The deep water data were combined with those obtained by Muttkowski for the purpose of getting a quantitative idea of the bottom fauna of the entire lake.

The macroscopic bottom fauna yielded 45 kilograms of dry organic matter per hectare; of this amount 33 kilograms consisted of protein, 4 kilograms of ether extract or fat and 8 kilograms of carbohydrate. While some of these organisms live more than one year, others pass through two or three generations in a year; the two groups of organisms are generally considered as balancing each other, so that the above quantities may be taken as the annual crop of this material as shown in table IV.

Considerable numbers of protozoa and other microscopic animals have been found in the bottom deposits, but no quantitative study of them has been made. It seems probable, however, that these minute forms would not add an appreciable amount of organic matter to the total weight of the bottom fauna.

*Fish.*—No accurate census of the fish caught by anglers in Lake Mendota each year has ever been made so that the assessment of this part of the biological crop can be estimated only roughly. Pearse and Achtenberg ('20) investigated this problem in connection with their studies of the yellow perch; they ·concluded that the annual catch consisted of something over 400,000 perch and about 5,600 other pan and game fish belonging to 7 different species. At the present time the perch population seems to be much smaller than it was at the time of their investigation; also the catches are now restricted by a closed season, by a size limit and by a limit on the number that can be taken each day by an angler. In view of these facts, the present catch probably does not exceed 200,000 per year. Based on the average weight of the perch usually caught by anglers, this

number represents an annual yield of 4 kilograms per hectare, live weight.

The average weight of the other pan and game fish amounts to about two kilograms per hectare, so that the total yield of pan and game fish is 6 kilograms per hectare. Carp are also fairly abundant in the lake and some of them are seined out each year in order to keep them under control. The average yield of carp between 1933 and 1936, inclusive, was 16 kilograms per hectare; adding the carp crop to that of the game and pan fish gives an annual fish yield of 22 kilograms per hectare, live weight. On a dry, ash-free basis, the total yield amounts to a little more than 5 kilograms per hectare as indicated in table IV. By far the greater part of this material consists of protein and fat.

*Energy Value of Annual Crop.*—Table IV shows that the total quantity of stored and accumulated energy in the form of dry organic matter in the annual crop of plants and animals amounts to 6,802 kilograms per hectare; of this quantity protein constitutes a little more than 2,804 kilograms, ether extract or fat 442 kilograms and carbohydrates 3,556 kilograms. On the basis of the energy equivalents of these three classes of organic matter, as indicated in a previous paragraph, the total energy value of the annual crop amounts to 346 gram calories per square centimeter of lake surface (table V).

TABLE V. *Energy values of the organic matter in the organisms, together with the estimated amounts of energy represented in their metabolism, and in the dissolved organic matter*

The values are stated in gram calories per square centimeter of lake surface. The results for phytoplankton and zooplankton are based on a turnover every two weeks during the year.

| | |
|---|---|
| Phytoplankton | 299 |
| Metabolism | 100 |
| Zooplankton | 22 |
| Metabolism | 110 |
| Bottom flora | 22 |
| Metabolism | 7 |
| Bottom fauna and fish | 3 |
| Metabolism | 15 |
| Dissolved organic matter | 71 |
| Total | 649 |

In addition to the organic material in the plants and animals, the water contains a certain amount of organic matter which cannot be recovered with a high speed centrifuge. It is either in true solution or is in such a finely divided state that it cannot be obtained with a centrifuge; for lack of a better term it has been called "dissolved organic matter" as compared with the "particulate organic matter" which can be recovered from the water with a centrifuge. The water of Lake Mendota contains 10 to 14 milligrams per liter, dry weight, of this dissolved organic matter; the mean of some 60 determinations is 12 milligrams per liter. When computed to an area basis, the average weight of this material is 1,523 kilograms per hectare, dry weight, of which 334 kilograms are protein, 68 kilograms fat and 1,121 kilograms carbohydrate. The energy value of this dissolved organic matter is about 71 gram calories per square centimeter.

*Utilization of Solar Energy.*—The chlorophyll-bearing aquatic plants are responsible for the utilization of the subsurface radiation; that is, the sun furnishes the power and the chlorophyll and associated pigments of the plants serve as the machines for the manufacture of the fundamental organic matter of the lake. Table IV shows that the phytoplankton and the large aquatic plants constitute the major item in the annual yield of biological material. Together they contribute 6,362 kilograms of dry organic matter per hectare as compared with 440 kilograms of zooplankton, bottom fauna and fish; that is, the plant contribution is 93 per cent and the animal part is 7 per cent of the total organic matter.

Table V gives the energy value of the various constituents of the annual biological crop. The two groups of plants, namely phytoplankton and large aquatics, have an energy value of 321 gram calories as compared with 25 gram calories per square centimeter in the animals. The 321 gram calories represented in the organic matter of the plants is only 0.27 of

one per cent of the mean annual radiation delivered to the surface of the lake, namely 118,872 calories. Two corrections need to be made in this result, however. (1) As already indicated some 28,500 calories of solar energy are lost at the surface of the water and thus do not reach the aquatic vegetation. Deducting this amount leaves 90,372 calories which pass into the water and thus become available for the plants. On this basis the percentage of utilization is increased to a little more than 0.35 of one per cent of the available radiation. (2) A certain amount of the organic matter synthesized by the plants is used in their metabolism and this does not appear in the percentage of utilization given above. Experiments show that some of the algae utilize in their metabolic processes about one-third of the organic matter that they synthesize. No data are available for the large aquatics, but assuming that they also utilize a similar proportion in their metabolism, the two groups of plants would represent a utilization of 428 calories which is equivalent to 0.47 of one per cent of the annual quantity of solar energy that actually enters the water.

This percentage is based on an average turnover in the phytoplankton every two weeks throughout the year, but there is some evidence that the turnover takes place more frequently, especially from April to October. With an average turnover once a week in the organic matter of the phytoplankton during the year, the energy value of this crop would be 798 calories, including metabolism; adding to this amount the 29 calories in the annual crop of bottom flora gives a total of 827 calories which is utilized by the plants. This is 0.91 of one per cent of the 90,372 calories of energy that penetrate the water and become available to the plants; in round numbers this may be regarded as a utilization of one per cent.

This small percentage of utilization of solar energy by aquatic plants shows that Lake Mendota is not a very efficient manufacturer of biological products in so

far as utilizing the annual supply of solar and sky radiation is concerned; on the other hand it belongs to the group of highly productive lakes.

While the aquatic plant crop appears to be inefficient in its utilization of solar energy, it compares very favorably with some of the more important land crops in this respect. Transeau ('26) states that only 1.6 per cent of the total available energy is used by the corn plant in photosynthesis during a growing period of 100 days, or from June 1 to September 8. Spoehr ('26) gives a table (p. 337) or Pütter's calculations for various crop plants in which the general average of the utilization of solar energy is about 3.0 per cent; summer wheat is given as 3.2 per cent, potatoes 3.0 per cent and beets 2.1 per cent. These computations for cultivated crops, however, take into account only the quantity of solar radiation available during comparatively brief growing periods and thus do not cover the entire year as indicated for the aquatic plants.

*Energy Value of Animals.*—The organic content of the animal population of the lake represents a conversion and further storage of the material manufactured by the plants, but no direct utilization of solar energy is involved in the transformation. It may be regarded as an expensive method of prolonging the existence of a certain portion of the original plant material. As previously indicated, it may take five grams of plant food to produce one gram of animal tissue, so that the plant equivalent of the animal crop may be reckoned as five times as large as the organic content of the animals; in the predatory animals, however, it would be much larger.

Table V shows that the energy value of the bottom and fish population is 25 gram calories per square centimeter; on the fivefold basis, this would represent the conversion of at least 125 gram calories of original plant organic matter. This utilization is approximately 40 per cent of the potential energy stored in the

annual plant crop of 321 gram calories which is based on a turnover in the phytoplankton every two weeks during the year. A turnover in the phytoplankton every week would give a plant crop of 620 calories and an animal utilization of a little more than 20 per cent.

*Dissolved Organic Matter.*—The energy value of the dissolved organic matter is indicated as 71 gram calories per square centimeter in table V. This material is constantly being supplied to the water by the various organisms and the standing crop of it remains fairly uniform in quantity during the different seasons of the year as well as in different years. While there is a regular turnover in this organic matter, it needs to be taken into account only once in computing the organic crop of the lake because it has its source in the plants and animals for which an annual yield has already been computed.

## Summary

1. The mean annual quantity of sun and sky radiation delivered to the surface of Lake Mendota over a period of 28 years was 118,872 gram calories per square centimeter of surface.

2. In the physical energy budget, the melting of the ice utilized 3,500 calories; the annual heat budget of the water was 24,200 calories and of the bottom 2,000 calories; the loss of energy by evaporation amounted to 29,300 calories; the surface loss by reflection, upward scattering and absorption was 28,500 calories and about 31,000 calories were lost by conduction, convection and radiation.

3. On the basis of a turnover in the organic content of the plankton every two weeks during the year, the energy value of the annual crop of plants and animals was 346 gram calories per square centimeter; of this amount, 321 calories were contributed by the plants and 25 calories by the animals. Adding to this the organic matter utilized by the plants and animals in their metabolic processes (232 calories) gives the annual crop an energy

value of 578 gram calories. In addition the dissolved organic matter had a value of 71 gram calories.

4. Assuming an average turnover of once a week in the organic matter of the phytoplankton, instead of every two weeks, would raise the energy budget of the annual crop of plants and animals to 977 gram calories, including the metabolized material. Adding the 71 calories in the dissolved organic matter gives a total of 1,048 calories in the biological energy budget.

5. An average turnover of once a week in the phytoplankton would give an annual utilization by these organisms and by the large aquatic plants of about one per cent of the sub-surface solar energy.

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# THE CYCLE FROM DOUGLAS FIR TO HEMLOCK

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## INTRODUCTION

It is somewhat of an anomaly that over much of the Douglas fir region—southern British Columbia, western Washington, and western Oregon—Douglas fir (*Pseudotsuga taxifolia*) is not the climax type. Forests of Douglas fir which now cover millions of acres would not persist as pure stands even if spared by fire and axe, but would make a gradual metamorphosis to forests of the shade-enduring species like western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and balsam firs (*Abies* spp.). A pure even-aged Douglas fir forest is evidence that a forest fire or a clear-cutting logging operation preceded the inception of the stand. Without such a clearance by fire or logging a Douglas fir forest would, in perhaps five or six centuries, be converted to the climax forest type—an uneven-aged stand of hemlock and other shade-tolerant trees.

The late C. S. Judd ('15), writing in 1915, says, "Douglas fir exists here only as a temporary type, which paradoxically would have utterly vanished long ago if it had not been for the purging effects of holocaustic fires." Other writers, Allen ('02), Clements ('20), Cheyney ('29), Frothingham ('09), McArdle ('30, '33), Westveld ('39), and Munger ('27, '30, '33), have mentioned the important rôle of fire in preserving the dominance of Douglas fir in Pacific Coast forests, but have offered little supporting evidence.

The paths of the great forest fires of the last century or two are plainly marked by even-aged stands, consisting to the extent of at least 90 per cent of Douglas fir (if within the preferred habitat of this tree), regardless of the proportion of Douglas fir in the original fire-killed stand. It has been estimated by the author that not over two-thirds of the uncut portion of the Douglas fir type carries mature or overmature stands; the remainder is covered by even-aged immature stands that followed fire.

## LIFE HISTORY OF A TYPICAL FOREST

Douglas fir is an aggressive and hardy tree. It produces some seed nearly every year; seeds in the cones or on the ground will, in part, survive even a severe crown fire in late summer. The seedlings establish themselves rather readily in spite of many adverse factors and usually make a new forest cover within a decade, dominating both brush and other species of trees. Sometimes in the new "fire forest" hemlocks, cedars, and balsam firs are absent for a few decades, even though indigenous to the locality. More often there are occasional specimens of these species mixed with the Douglas fir. As the even-aged Douglas fir forest on an old burn continues its growth hemlocks, cedars, and balsam firs make their appearance in the understory. These tolerant species can survive where Douglas fir reproduction would not. The seed source of these invaders is sometimes a mystery, when, as may happen, few parent trees are in evidence. By the time the Douglas firs are a century old there is often a conspicuous understory of tolerant conifers.

In its second century the Douglas fir stand thins out a good deal. Occasional trees die from wind, snow-breakage, insects, or disease, and this gives the tolerant species an opportunity for expansion. By the end of this century the invading hemlocks, etc., have definitely won a place in the main stand. At 300 years the tolerant trees may outnumber the Douglas firs. The latter are mature, are no longer making significant height growth, and one by one are succumbing to casualties. No young Douglas firs take their place, for the canopy is much too dense;

instead, there are hemlocks, cedars, lowland white firs (*Abies grandis*), and silver firs (*Abies amabilis*) ready to fill in any gaps. At 400 or 500 years the Douglas firs are becoming senile and are fast disappearing as the result of centuries of buffeting by the elements and disease.

## EXAMPLES OF SUCCESSION FROM DOUGLAS FIR TO HEMLOCK

*A Late Stage in the Succession.*—A stand on the Wynoochee River on the south side of the Olympic National Forest illustrates well a rather late stage of this succession. Here is a forest of 590-year-old Douglas firs, most of them from 60 to 100 inches in diameter and from 250 to 275 feet tall. There are only 5.8 living trees of this kind to the acre but there are many dead standing and fallen Douglas fir giants—evidence that formerly the forest was composed of numerous Douglas firs of this generation which have now succumbed to "old age," windfall, or the gradual inroads of decay organisms. There are no smaller or younger Douglas firs. Associated with and largely beneath the veteran Douglas firs are 21.9 hemlocks per acre over 16 inches in diameter, most of them under 40 inches in diameter, and none over 60. In addition, there are many small hemlocks from 16 inches in diameter down to suppressed seedling size. They are distinctly younger than the Douglas fir and uneven in age. The Douglas firs are nearly all within 25 years, plus or minus, of being 590 years old, as proven by ring counts on the stumps of a 160-acre sample plot. The youngest of the hemlocks (over 16 inches in diameter) is 130 years old and the oldest 525. The ages of the hemlocks on the same sample plot, as determined after logging, are distributed by centuries as follows:

|  |  |
|---|---|
| 101–200 years old | 28 per cent |
| 201–300 years old | 25 per cent |
| 301–400 years old | 44 per cent |
| over 400 years old | 3 per cent. |

The structure of this typical forest that is passing from fir to hemlock is shown in table I.

TABLE I. *Composition by diameter groups in a forest on the Olympic National Forest where there has been no fire for at least 550 years*

| | Number of trees per acre | | |
|---|---|---|---|
| Diameter class inches | *Pseudotsuga taxifolia* (Douglas fir) | *Tsuga heterophylla* (western hemlock) | *Thuja plicata* (western red cedar) and *Abies amabilis* (silver fir) |
| 16–20 | — | 4.62 | .09 |
| 21–40 | .06 | 14.44 | — |
| 41–60 | 1.34 | 2.81 | .06 |
| 61–80 | 3.41 | — | .19 |
| Over 80 | .97 | — | .03 |
| Total | 5.78 | 21.87 | .37 |

It is not uncommon to find in western Washington and northwestern Oregon on sites eminently suited to Douglas fir, stands of hemlock, etc., containing no living specimens of Douglas fir but perhaps having standing dead trees or windfalls of this species to give proof of its former presence. This condition typifies probably the final stage of this succession.

*Decrease of Douglas Fir with Age of Stand.*—A strip survey of the western two-thirds of Lewis County, Washington, in the heart of the Douglas fir region, illustrates well the invasion by hemlock and other tolerant species of stands that start as almost pure Douglas fir. On a series of quarter-acre plots, spaced arbitrarily on over a hundred miles of survey lines, the forest type and all the living trees over two inches in diameter were recorded by diameter. Plots containing more than 60 per cent of Douglas fir were classed as belonging to the Douglas fir type, which in turn was divided into five age (or size) classes.

Type 6 = Douglas fir, large old growth

Type 7 = Douglas fir, small old growth

Type 8 = Douglas fir, large second growth

Type 9 = Douglas fir, small second growth

Type 10 [1] = Douglas fir, seedlings and saplings.

As shown in table II, hemlock, cedar, etc., are outnumbered by Douglas fir nearly four to one in the youngest age group; of the trees over 14 inches in diameter there is only one hemlock, etc., to every three acres, while there are five Douglas firs to the acre. The tolerant species become more numerous in relation to the Douglas fir in each successively older age class, so that in mature old-growth stands there are approximately two and a half times as many hemlocks, etc., as Douglas firs of all sizes, and of the trees over 14 inches in diameter there are almost as many hemlocks, etc., as Douglas firs.

TABLE II. *Occurrence of Douglas fir and of hemlock, etc., in stands of various age classes, Lewis County, Washington*

| Diameter class inches | Age classes of Douglas fir type | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Type 10 Seedlings and saplings 83 plots | | Type 9 Small second growth 380 plots | | Type 8 Large second growth 426 plots | | Type 7 Small old growth 27 plots | | Type 6 Large old growth 502 plots | |
| | Number of trees per acre | | | | | | | | | |
| | DF | Hem. | DF | Hem. | DF | Hem. | DF | Hem. | DF | Hem. |
| 2–14 | 419 | 123 | 246 | 117 | 27 | 27 | 2 | 32 | 3 | 35 |
| Over 14 | 5 | .3* | 23 | 1 | 52 | 7 | 39 | 27 | 19 | 18 |
| All sizes | 424 | 123 | 269 | 118 | 79 | 34 | 41 | 59 | 22 | 53 |
| Per cent of total | 78 | 22 | 70 | 30 | 70 | 30 | 41 | 59 | 29 | 71 |

\* A fraction of a tree per acre. Elsewhere in this table fractions of trees have been disregarded.

The progressive increase of hemlock and other tolerant species as Douglas fir forests grow older can be shown by further subdividing one of the five broad age

[1] The numbers are those attached to the more than 50 types and age classes recognized in the forest survey of the Douglas fir region.

classes into age groups of about two decades each. The Lewis County sample plots, located in Forest Survey Type 8—large second-growth, which roughly covers stands from about 50 to 160 years old—were resubdivided into four age groups. For each group the number of Douglas firs and of hemlocks, etc., both smaller and larger than 14 inches in diameter on the average acre, is shown in table III. It is noticeable that there is

TABLE III. *The occurrence of Douglas fir and of hemlock, etc., in "large second growth" type of various ages; Lewis County, Washington*

| Diameter class inches | Age of "large second growth" stands | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Under 70 years 83 plots | | 70–89 years 145 plots | | 90–109 years 72 plots | | Over 110 years 298 plots | |
| | Number of trees per acre | | | | | | | |
| | DF | Hem. | DF | Hem. | DF | Hem. | DF | Hem. |
| 2–14 | 43 | 19 | 41 | 32 | 20 | 28 | 14 | 29 |
| Over 14 | 49 | 3 | 61 | 7 | 56 | 8 | 54 | 9 |
| All sizes | 92 | 22 | 102 | 39 | 76 | 36 | 68 | 38 |
| Per cent of total | 81 | 19 | 72 | 28 | 68 | 32 | 64 | 36 |

a gradual, though not regular, falling off in the total number of Douglas firs as the stands increase in age and an even more noticeable increase in the number of hemlocks. The diminishing ratio of Douglas firs to hemlocks is most striking with the 2–14 inch trees—the understory trees. In the stands under 70 years of age there are more than twice as many Douglas firs as hemlocks, etc., while in the age group over 110 years the relationship is reversed. It would seem logical to assume that the old stands had the same composition in their youth that the young stands now have. Based on this assumption the difference in composition between young and old stands can be logically attributed to the strong tendency for hemlock to replace Douglas fir unless fire or logging check this natural ecological process.

*All Stages of Succession Found in One Valley.*—Figures 1 to 4 portray four stands, all within a few miles of each other, in the Wind River Valley, Washington, and all similar with respect to soil and elevation. They exemplify the full cycle from Douglas fir saplings to hemlock veterans. Figure 1 shows a dense even-aged stand of saplings practically all Douglas firs. Figure 2 is a 99-year-old stand in which the main canopy is practically pure Douglas fir but in which hemlocks are beginning to appear in the understory. Figure 3 is a view in a stand averaging 300 to 400 years old where hemlocks are beginning to replace the aging Douglas firs. Figure 4 illustrates the last and final stage of this forest drama where the Douglas fir is all but gone and hemlocks and other tolerant species of all sizes and ages make up the stand. Undoubtedly the forests por-trayed in figures 3 and 4 once had the appearance of the pure fir stands shown in figures 1 and 2.

*Early Stage of Succession Found in Immature Stands.*—Sample plots in even-aged immature stands of Douglas fir which are periodically reexamined to de-termine growth, mortality, and changes in stand structure show very convincingly the early stages of the invasion by hem-lock. On the Willamette National Forest three acres of plots established in a 54-year-old stand 30 years ago had then only one hemlock over two inches in diameter. Now there are eight over three inches in diameter, all in the understory; yet there are no understory Douglas firs younger than the main stand. Though Douglas fir seed germinates on the forest floor after each seed crop, the seedlings, in contrast to those of hemlock, are not able to survive in the shade.



FIG. 1. Sapling stand of almost pure Douglas fir on lands recently clear cut. (This and the other figures are all from the Wind River Experimental Forest, Washington, within a few miles of each other, on similar sites, and at approximately the same altitude.)
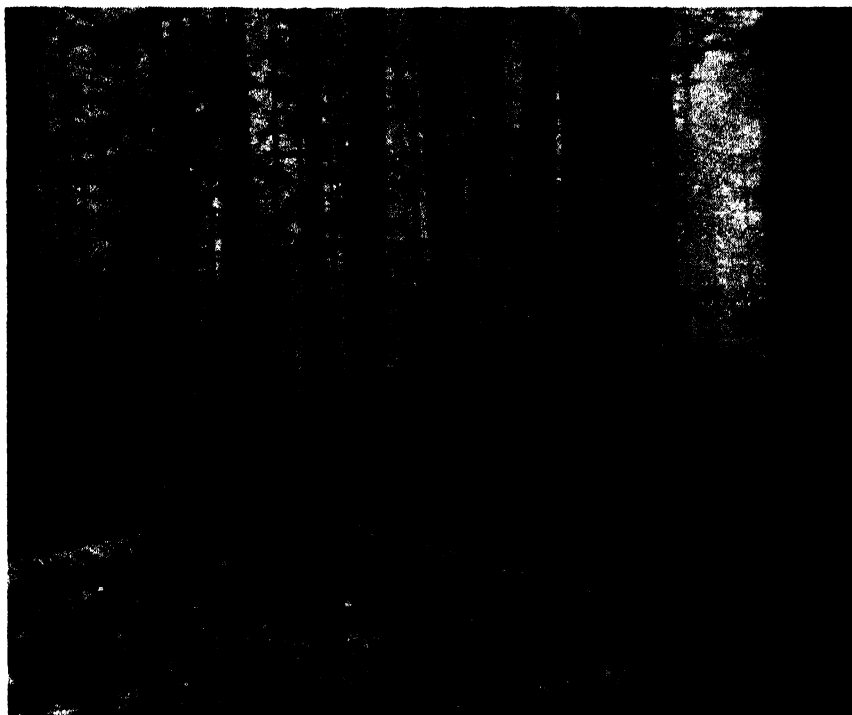
FIG. 2. A 99-year-old forest of almost pure Douglas fir, in which western hemlock is beginning to appear in the understory.

FIG. 3. A 350–400-year-old forest with many dead and decadent Douglas firs, whose places are being taken by thrifty western hemlocks.
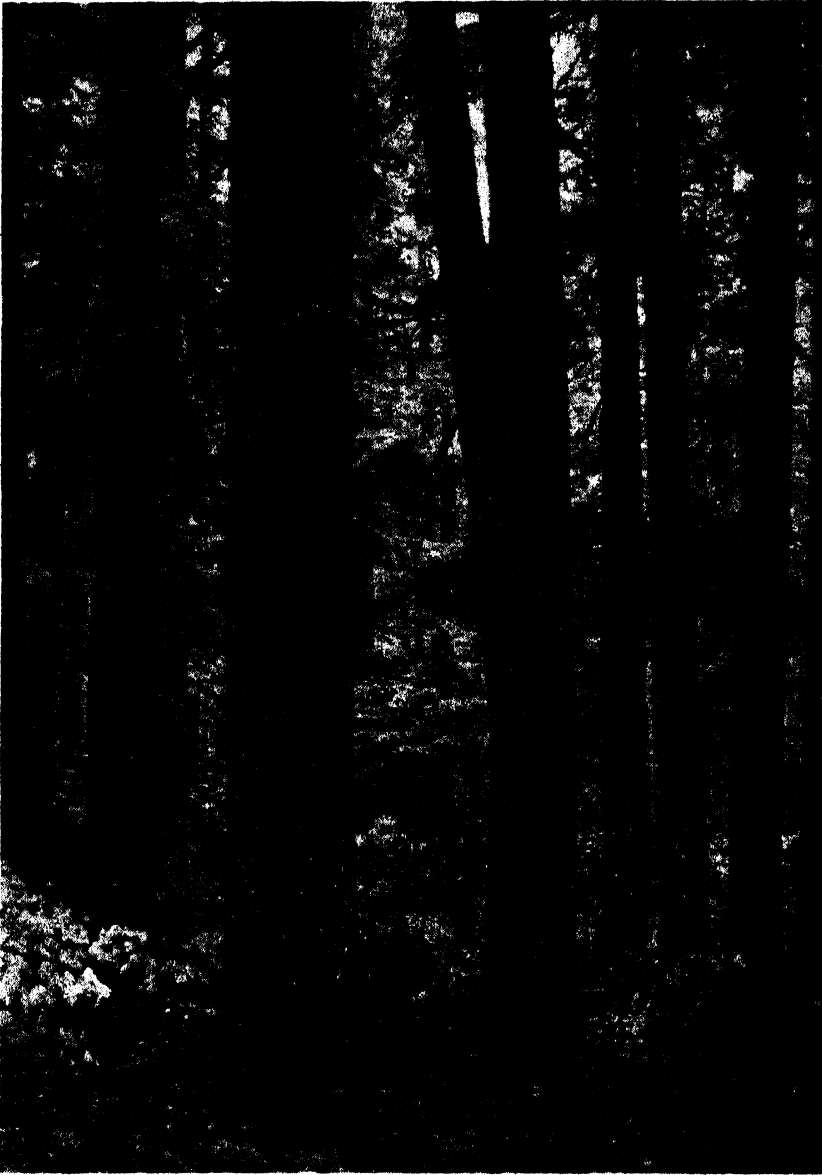
FIG. 4. A forest of uneven-aged western hemlock, not visited by fire for several centuries, in which there is only an occasional relic of the former Douglas fir stand.

PREVALENCE OF THE NON-CLIMAX TYPE IN WESTERN WASHINGTON

The Forest Survey [2] indicates that there are in that portion of the Douglas fir region within the State of Washington approximately 4 million acres of virgin

[2] "Forest resources of the Douglas fir region," by H. J. Andrews and R. W. Cowlin. 1934. Unpublished Ms.

mature or overmature forest—exclusive of the high mountain forests. It is consistent with the theory of succession from Douglas fir to hemlock and other shade-tolerant trees to assume that nearly all this area might be covered with the climax species. had there been no fires for several centuries. On the other hand, it is equally possible that most of this area might now be covered with Douglas fir

type had prehistoric fires staged the right ecological condition. Yet only 58 per cent of this old forest is classed as either hemlock, cedar, or spruce type, the remaining 42 per cent, or 1,700,000 acres, being mature Douglas fir type.

In addition to the old growth there are in western Washington 3½ million acres of immature Douglas fir type, mostly on cut-over land or on burns that occurred within the last century and a half. In contrast, there are less than a half-million acres of immature hemlock, cedar, and spruce types, and that mostly within the "fog belt," where Douglas fir is not supreme.

Another group of sample plots on the east side of the Olympic Peninsula, established in 1926 in a 51-year-old Douglas fir stand, is already beginning to experience the invasion of the tolerant conifers. The main canopy was, in 1926, and still is. about 100 per cent Douglas fir, but 10 or 15 per cent by number of all the trees are small suppressed hardwoods and tolerant conifers. In the last decade an average of 4.5 hemlocks and cedars per acre have grown into the 3-inch diameter class, while no Douglas firs have so developed. Furthermore, many of the smaller Douglas firs have died. Thus, the proportion of tolerant conifers over the intolerant Douglas fir is gradually increasing even in this young stand. It is evident then that the process of conversion from pure Douglas fir to hemlock, cedar, etc., that takes perhaps five centuries to complete, may begin in the first half century of the life of the Douglas fir forest.

### SUCCESSION FROM DOUGLAS FIR TO HEMLOCK NOT UNIVERSAL IN THIS REGION

Notwithstanding all the foregoing evidence, the replacement of Douglas fir by hemlock and its associates is not the inevitable climax, barring fire and cutting, throughout the whole Douglas fir region. This is not at all a homogeneous region,

for it has a great range in climate from British Columbia to southern Oregon and from the Pacific shore line to the crest of the Cascade Range. The dominance of the species varies in different parts of the region, and in certain districts neither hemlock, cedar, nor any of the balsam firs seems to be the climax tree.

Along the ocean there is a strip 25 miles wide in northern Washington and tapering off to nothing half way down the Oregon coast where Douglas fir has little place in forest succession. Here hemlock and Sitka spruce are predominant in both young and old stands, and apparently maintain their dominance in spite of fire and logging throughout the life cycle of a stand.

Hanzlik ('32) calls attention to the fact that on the western and southern slopes of the Olympic Mountains of Washington silver fir (*Abies amabilis*) and not western hemlock seems to be the climax type. He finds that in this locality on areas once covered largely with Douglas fir, and which have been free from fire for several centuries, the Douglas fir gradually disappears. As the veterans of the original stand die, they are replaced by hemlocks which have come up in the understory. He believes that they, being short lived, are in turn replaced by the even more tolerant silver fir, which then holds the ground against all intruders— until fire or axe makes a clearing.

Hemlock, western red cedar, noble fir, and silver fir all require moister and cooler sites than are necessary for Douglas fir. Hence, these species diminish in frequency from north to south or with a decrease in altitude, and are almost absent in stands of any age in the drier valley and foothill lands of western Oregon. The old Douglas fir forest in west-central and southwestern Oregon is, therefore, not likely to be replaced by hemlock— even if it escapes fire for a few centuries. As the veterans in an even-aged pure Douglas fir stand die, young Douglas firs may fill the gaps, or broad-leaf shrubs may take possession temporarily, or low-

land white fir may become dominant. Under some circumstances the climax might be an uneven-aged stand in which Douglas fir predominates or in other cases a mixed stand of Douglas fir and other intolerant and tolerant conifers. It is difficult to say what the climax type really is for the dry situations of western Oregon, so few stands have escaped for long the inroads of fire.

Over much of the so-called Douglas fir region, however, pure Douglas fir may be considered to be a temporary type, the consequence of fire or logging that cleared the ground for this aggressive and light-demanding tree. Over most of western Washington and northwestern Oregon, except in some dry valleys and on moraines, the shade-tolerant hemlock, cedar, and balsam firs would probably have dominated the forests which David Douglas and other early explorers found had there been no holocausts in the preceding thousand years.

## SUMMARY

Douglas fir, the predominant tree in southern British Columbia, western Washington, and Oregon, is not the climax species. It is a light-requiring, aggressive tree that forms pure even-aged stands after fire or logging but does not reproduce in its own shade. In the absence of fire or clear-cut logging western hemlock and other shade-tolerant trees reproduce in the shelter of the virgin trees and ultimately supplant Douglas fir if present. This process is traced by citing the composition of forests of various ages. As even-aged stands of Douglas fir increase in age the proportion of Douglas fir diminishes while that of hemlock and other tolerant trees increases. The invasion of hemlock in immature stands of Douglas fir is also shown by permanent sample plot records.

A forest on the Olympic Peninsula that has been free of fire for over 5 centuries and once consisted largely of even-aged Douglas fir, is shown now to have only 5.8 living Douglas firs per acre but 21.9 large hemlocks (and many small hemlocks) per acre which are all younger than the Douglas firs. The young Douglas fir stands in Lewis County were found to consist by number of trees of 78 per cent Douglas fir and 22 per cent hemlock, while in old stands the proportion was reversed. Immature Douglas fir type stands show a decrease of 17 per cent in the proportion of Douglas fir and a corresponding increase in the proportion of hemlock and other tolerant trees from age class "under 70" to age class "over 110." In western Washington only 58 per cent of the area of old-growth virgin forest that might be expected to be of the climax type is so classed, the remainder being of the temporary type, Douglas fir.

While this ecological cycle from Douglas fir to hemlock etc. seems to be general in the moister and cooler parts of the Douglas fir region, it does not obtain in the southern part of the region which is less favorable for hemlock, cedar, and balsam firs. Likewise, close to the coast Douglas fir has little place in forest succession, western hemlock and Sitka spruce being predominant in both young and old stands.

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# THE FIT AND SIGNIFICANCE OF CONTAGIOUS DISTRIBUTIONS WHEN APPLIED TO OBSERVATIONS ON LARVAL INSECTS

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## INTRODUCTORY

The present work is a test of the applicability to entomological data of the contagious distributions of Neyman ('39), which may be regarded as a generalization of the Poisson distribution for the case of organisms dispersing from randomly distributed groups. Supposing that the eggs of an insect would be laid in small groups called egg masses from which emerging larvae would disperse independently and employing certain simplifying assumptions, Neyman has found the probability of 0, 1, 2, etc. larvae occurring on a given unit area. In the special case, when each mass consists of only one egg, the Poisson distribution arises. The contagious distributions of Pólya ('31) are also considered in the present work.

Neyman supposes $N$ egg masses are laid on a total area, $M$, where not the absolute magnitude of $N$ and $M$ but that of their ratio, $\alpha = N/M$, is of concern. Let the average number of larvae surviving from an egg mass at the time when the counts are made be $\beta$. It is desired to find the probable number of larvae, on a unit area, $w$, within $M$. It is assumed, in view of the limited duration of the larval stage, that the larva is capable of a limited movement so that there is an area, $\Gamma$, from which the larvae found in $w$ must have come. Neyman has developed, for the number of larvae per unit area, several distributions which he calls Type A, with 2 or 3 parameters, and Types B and C, with 2 parameters. Results from the fitting of Type A with 3 parameters are discussed by Neyman ('39). The present discussion is limited to a comparison of the 3 types with 2 parameters. Each type is most conveniently expressed in terms of a pair of arbitrary parameters which are functions of $\alpha$, $\beta$, and $\Gamma$, termed hereafter biological constants.

The distribution of Type A can be conveniently treated in terms of the parameters, as in Neyman's equations (40),

$$m_1 = \alpha\Gamma, \tag{1}$$

$$m_2 = \beta/\Gamma. \tag{2}$$

Then from Neyman's equation (45), the probability that the number, $X$, of insects occurring on a given unit area will be $n$, is given by

$$P\{X=n\} = e^{-m_1} \frac{m_2^n}{n!} \frac{d^n}{du^n} e^{m_1 e^{u-m_2}} \Big]_{u=0}. \tag{3}$$

The calculations from (3) become laborious as the value of $n$ becomes great, but as is discussed by Neyman ('39) we can put this equation in the recurrent form,

$$\begin{aligned} P\{X=n+1\} \\ = \frac{m_1 m_2 e^{-m_2}}{n+1} \sum_{k=0}^{n} \frac{m_2^k}{k!} P\{X=n-k\}, \end{aligned} \tag{4}$$

where we start with

$$P\{X=0\} = e^{-m_1(1-e^{-m_2})}. \tag{5}$$

in fitting Type A to an empirical distribution consider the moments,

$$\mu_1' = \alpha\beta, \tag{6}$$

*i.e.*, the mean number of larvae per unit area is simply the mean number of egg masses per unit area times the average number of survivors per egg mass, and, as in Neyman's equation (50),

$$\mu_2 = \alpha\beta + \alpha\beta^2/\Gamma, \tag{7}$$

when from our (1), (2), (6) and (7),

$$\mu_1' = m_1 m_2, \tag{8}$$

$$\mu_2 = m_1 m_2 (1 + m_2). \tag{9}$$

Since, from (8) and (9),

$$m_1 = \mu_1'^2/(\mu_2 - \mu_1'), \qquad (10)[1]$$

$$m_2 = (\mu_2 - \mu_1')/\mu_1', \qquad (11)$$

we can estimate the constants, $m_1$ and $m_2$, by putting in (10) and (11) the first two empirical moments.

In the course of the derivation of Type A, Neyman made certain mathematical simplifications, but fearing he had perhaps over-simplified the work he also developed more involved distributions which he called his Types B and C. He remarked that "The comparative merits of all these distributions could be judged by comparing them with the results of observation"; such is one of the main purposes of the present work.

For Types B and C

$$P\{X = n\} = \frac{1}{n!} \frac{d^n \psi(z)}{dz^n} \Big]_{z=0}, \qquad (12)$$

where from Neyman's equation (92) for Type B the appropriate generating function is

$$\psi(z) = e^{-m_1'} e^{m_1' \frac{e^{m_2'(z-1)} - 1}{m_2'(z-1)}}, \qquad (13)$$

when, as in Neyman's equations (91),

$$m_1' = \alpha \Gamma, \qquad (14)$$

$$m_2' = 2\beta/\Gamma. \qquad (15)$$

From our (12)

$$P'\{X = 0\} = e^{-\frac{m_1'}{m_2'}(e^{-m_2'} - 1 + m_2')}, \qquad (16)$$

but for values of $n > 0$ it is desirable to reduce the calculations from (12) to a recurrent form analogous to (4). Following the procedure of Neyman ('39:50) in finding a recurrent expression we get

$$P'\{X = n+1\} = \frac{m_1'}{(n+1)m_2'} \sum_{k=0}^{n} (k+1)$$

$$\times \left(1 - e^{-m_2'} \sum_{s=0}^{k+1} \frac{m_2'^s}{s!}\right) P\{X = n-k\}. \qquad (17)$$

To fit Type B we note that the first moment is again as in (6) while the second moment can be obtained from Neyman's general formulae (35) by substituting from his equation (88) when, in his symbols,

$$P_n = M_n' = \frac{1}{n+1} \left(\frac{2}{\Gamma}\right)^n, \qquad (18)$$

whence, in our symbols,

$$\mu_2 = \alpha\beta + 4\alpha\beta^2/3\Gamma. \qquad (19)$$

From our (6), (14), (15) and (19),

$$\mu_1' = m_1' m_2'/2, \qquad (20)$$

$$\mu_2' = m_1' m_2'(1 + 2m_2'/3)/2 \qquad (21)$$

and from (10), (11), (20), and (21), we estimate

$$m_1' = 4m_1/3, \qquad (22)$$

$$m_2' = 3m_2/2. \qquad (23)$$

The distribution of Type C is again derived from (12) when, from Neyman's equation (95),[2] the appropriate generating function is

$$\psi(z) = e^{-m_1''} e^{2m_1'' \frac{e^{m_2''(z-1)} - 1 - m_2''(z-1)}{m_2''^2(z-1)^2}}, \qquad (24)$$

when, as in Neyman's equations (94),

$$m_1'' = \alpha\Gamma, \qquad (25)$$

$$m_2'' = 3\beta/\Gamma. \qquad (26)$$

Following for Type C the treatment indicated in connection with Type B,

$$P''\{X = 0\}$$
$$= e^{2\frac{m_1''}{m_2''^2}\left(e^{-m_2''} - 1 - \frac{m_2''^2}{2} + m_2''\right)}, \qquad (27)$$

and for $n > 0$, it is again desirable to reduce the calculations to a recurrent form, namely,

$$P''\{X = n+1\} = \frac{2m_1'' e^{-m_2''}}{(n+1)m_2''^2} \sum_{k=0}^{n} (k+1)$$

$$\times \left\{ m_2''\left(e^{m_2''} - \sum_{s=0}^{k} \frac{m_2''^s}{s!}\right) - (k+2)\left(e^{m_2''}\right.\right.$$

$$\left.\left. - \sum_{s=0}^{k+1} \frac{m_2''^s}{s!}\right)\right\} P\{X = n-k\}. \qquad (28)[3]$$

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[1] When $m_1$ is estimated as in (10), $m_1^{-\frac12}$ is the Charlier coefficient of disturbance, discussed by Beall ('35).

[2] Misprinted in original paper.

[3] The recurrent equations (17) and (28) are due

For Type C, the first moment is as in our (6) and from Neyman's general formulae (35) with his equation (89),

$$\mu_2 = \alpha\beta + 3\alpha\beta^2/2\Gamma. \qquad (29)$$

From our (6), (25), (26) and (29),

$$\mu_1' = m_1''m_2''/3, \qquad (30)$$

$$\mu_2 = m_1''m_2''(1 + m_2''/2)/3. \qquad (31)$$

Whence from (10), (11), (30) and (31), we estimate

$$m_1'' = 3m_1/2, \qquad (32)$$

$$m_2'' = 2m_2. \qquad (33)$$

## The Agreement between Neyman's Distributions and some Data from Experimental Work

Neyman's distributions were fitted to 11 populations as obtained from 3 experiments in the field on insecticides, in order to compare theoretical anticipation with observations.

First, the distributions were fitted to the data from an experiment on the beet webworm, *Loxostege sticticalis* L., which lays masses as small as 1 and seldom exceeding 5 eggs. The larvae are reported often to mature on the plant on which they have hatched although they can. move freely. The webworms, which were considered, consisted mainly of mature larvae and of some half grown. Counts, shown in table VI, were made on the number of larvae of this insect present on unit areas of 3 ft. of row. Each experimental plot contained 25 such unit areas and there were 4 treatments in 13 replications. If possible heterogeneity of the area with respect to the laying of eggs is neglected, the 325 unit areas subjected to each treatment should constitute an example of the distributions covered by the theory of Neyman. Using estimates of $m_1$, $m_2$, $m_1'$, $m_2'$, etc. from (10), (11), (22) etc., for each such empirical distribution the

to Professor J. Neyman. Without this simplification, it would be practically impossible to compute the distributions concerned.

TABLE I. *Observations from an experiment on Loxostege sticticalis L. and the fitted distributions of Neyman's types, A, B and C*

| Class | Treatment 1 (Untreated) | | | | Treatment 2 | | | | Treatment 3 | | | | Treatment 4 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. |
| 0 | 117 | 116.7 | 115.8 | 115.3 | 205 | 203.8 | 203.7 | 203.7 | 162 | 157.6 | 157.3 | 157.2 | 227 | 226.2 | 226.1 | 226.0 |
| 1 | 87 | 84.3 | 86.0 | 86.9 | 84 | 87.8 | 87.9 | 88.0 | 88 | 96.0 | 96.5 | 96.8 | 70 | 71.7 | 72.0 | 72.1 |
| 2 | 50 | 58.3 | 57.9 | 57.8 | 30 | 25.9 | 25.8 | 25.7 | 45 | 45.4 | 45.1 | 45.0 | 21 | 20.8 | 20.6 | 20.5 |
| 3 | 38 | 33.6 | 33.3 | 33.1 | 4 | 6.1 | 6.0 | 6.0 | 23 | 17.6 | 17.5 | 17.4 | 6 | 5.0 | 5.0 | 5.0 |
| 4 | 21 | 17.4 | 17.3 | 17.2 | 2 | 1.2 | 1.2 | 1.2 | 5 | 6.0 | 6.0 | 6.0 | 1 | 1.1 | 1.1 | 1.1 |
| 5 | 7 | 8.3 | 8.3 | 8.2 | | | | | 2 | | | | | | | |
| 6 | 2 | 3.7 | 3.7 | 3.7 | | | | | | | | | | | | |
| 7 | 2 | 1.6 | 1.6 | 1.6 | | | | | | | | | | | | |
| 8 | 0 | | | | | | | | | | | | | | | |
| 9 | 1 | +1.1 | +1.1 | +1.2 | +.2 | +.4 | +.4 | +2.4 | +2.6 | +2.6 | +.2 | +.2 | +.3 | | | |
| $P_{\chi^2}$ | | .543 | .548 | .533 | .282 | .273 | .264 | .269 | .235 | .219 | .726 | .704 | .714 | | | |

probability of various numbers, 0, 1, 2, etc., of larvae per unit area were calculated from (4), (5), (16), (17), (27) and (28), for Neyman's Types A, B, and C, with the results shown in table I. The departures of the observations from each theoretical distribution gave a value of $\chi^2$ of which the probability was, for convenience of reference, associated with a given theoretical distribution in the table. As can be seen Types A, B and C, fitted with almost equal excellence.

The theory was further applied to the experimental data of Stirrett, Beall and Timonin ('37) on the European corn borer, *Pyrausta nubilalis* Hubn., which lays masses of about 20 eggs. The larvae had had two possible periods of migration prior to the examination which was made on October 19. Since the larvae had hatched in July and reached full growth in August the population was effectively of one age. Counts were made on the number of borers on the unit areas occupied by a hill of corn. Each

plot contained 64 hills of which 8 were chosen randomly and examined. Since there were 4 treatments in 15 replications, there were 4 distributions each of 120 observations.

Neyman's Type A was fitted to the data on *P. nubilalis* as it had been fitted to the data shown in table I with the results indicated by $P_{\chi 2}$ in table II. It can be seen that the observed distributions were approached but not fitted well by the theory. It was felt that this poorness of fit arose because the chance variation in the empirical frequencies for the relatively improbable higher classes unduly influenced both the moments and the fit. Accordingly, in these classes the observations were smoothed a little by eye to give adjusted empirical distributions, which are shown in table II, and from these, new adjusted moments were calculated and new theoretical distributions of Types A, B and C, were calculated for comparison with the observed distributions, as shown in table III.

TABLE II.   *Neyman's distribution of Type A fitted to observations from an experiment on Pyrausta nubilalis Hubn., and in addition arbitrarily smoothed observations*

| Class | Treatment 1 (Untreated) | | | Treatment 2 | | | Treatment 3 | | | Treatment 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | A Exp. | Obs. sm'd | Obs. | A Exp. | Obs. sm'd | Obs. | A Exp. | Obs. sm'd | Obs. | A Exp. | Obs. sm'd |
| 0 | 19 | 34.4 | 19 | 24 | 22.6 | 24 | 43 | 49.8 | 43 | 47 | 53.4 | 47 |
| 1 | 12 | 6.4 | 12 | 16 | 16.7 | 16 | 35 | 23.3 | 35 | 23 | 19.7 | 23 |
| 2 | 18 | 10.4 | 18 | 16 | 18.3 | 16 | 17 | 18.9 | 17 | 27 | 17.5 | 27 |
| 3 | 18 | 11.9 | 18 | 18 | 16.4 | 18 | 11 | 12.3 | 11 | 9 | 12.1 | 9 |
| 4 | 11 | 11.2 | 11 | 15 | 13.4 | 15 | 5 | 7.3 | 5 | 7 | 7.5 | 7 |
| 5 | 12 | 9.5 | 12 | 9 | 10.3 | 9 | 4 | 4.1 | 4 | 3 | 4.4 | 3 |
| 6 | 7 | 7.9 | 9 | 6 | 7.5 | 6 | 1 | ⎧ 2.2 | 2 | 1 | ⎧ 2.5 | 2 |
| 7 | 8 | 6.4 | 6 | 5 | 5.2 | 5 | 2 | ⎨ 1.1 | 1 | 1 | ⎨ 1.4 | 1 |
| 8 | 4 | ⎧ 5.2 | 4 | 3 | ⎧ 3.5 | 4 | 2 | ⎩ +1.0 | 1 | 0 | ⎩ +1.5 | 1 |
| 9 | 4 | ⎨ 4.1 | 3 | 4 | ⎨ 2.3 | 3 | | | 1 | 0 | | |
| 10 | 1 | ⎨ 3.2 | 2 | 3 | ⎧ 1.5 | 2 | | | | 1 | | |
| 11 | 0 | ⎨ 2.5 | 1 | 0 | ⎨ | 1 | | | | 1 | | |
| 12 | 1 | ⎨ 1.9 | 1 | 1 | ⎩ +2.3 | 1 | | | | | | |
| 13 | 1 | ⎨ 1.4 | 1 | | | | | | | | | |
| 14 | 0 | | 1 | | | | | | | | | |
| 15 | 1 | ⎩ +3.6 | 1 | | | | | | | | | |
| 16 | 0 | | 0 | | | | | | | | | |
| 17 | 1 | | 1 | | | | | | | | | |
| 18 | 0 | | | | | | | | | | | |
| 19 | 1 | | | | | | | | | | | |
| 26 | 1 | | | | | | | | | | | |
| $P_{\chi^2}$ | | .002 | | | .978 | | | .093 | | | .088 | |

TABLE III. *Neyman's distributions of Types A, B and C, fitted to arbitrarily smoothed observations on Pyrausta nubilalis Hubn., shown against the observed distributions*

| Class | Treatment 1 (Untreated) | | | | Treatment 2 | | | | Treatment 3 | | | | Treatment 4 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. |
| 0 | 19 | 23.2 | 21.2 | 20.2 | 24 | 22.8 | 21.6 | 21.0 | 43 | 50.2 | 49.2 | 48.7 | 47 | 46.5 | 45.9 | 45.6 |
| 1 | 12 | 11.6 | 14.1 | 15.0 | 16 | 16.7 | 18.2 | 18.9 | 35 | 23.0 | 24.7 | 25.5 | 23 | 26.8 | 28.0 | 28.6 |
| 2 | 18 | 14.8 | 15.0 | 15.3 | 16 | 18.3 | 18.4 | 18.5 | 17 | 18.8 | 18.4 | 18.3 | 27 | 20.1 | 19.8 | 19.8 |
| 3 | 18 | 14.5 | 14.3 | 14.3 | 18 | 16.4 | 16.3 | 16.3 | 11 | 12.3 | 12.0 | 11.8 | 9 | 12.4 | 12.2 | 12.1 |
| 4 | 11 | 12.7 | 12.6 | 12.5 | 15 | 13.4 | 13.3 | 13.2 | 5 | 7.3 | 7.2 | 7.1 | 7 | 7.0 | 6.9 | 6.8 |
| 5 | 12 | 10.6 | 10.6 | 10.5 | 9 | 10.3 | 10.1 | 10.1 | 4 | 4.1 | 4.1 | 4.0 | 3 | 3.7 | 3.7 | 3.6 |
| 6 | 7 | 8.6 | 8.5 | 8.4 | 6 | 7.5 | 7.4 | 7.3 | 1 | 2.2 | 2.2 | 2.2 | 1 | 1.8 | 1.8 | 1.8 |
| 7 | 8 | 6.7 | 6.6 | 6.5 | 5 | 5.2 | 5.2 | 5.1 | 2 | 1.1 | 1.2 | 1.2 | 1 | .9 | .9 | .9 |
| 8 | 4 | 5.1 | 5.0 | 5.0 | 3 | 3.5 | 3.5 | 3.5 | 2 | +1.0 | +1.0 | +1.2 | 0 | +.8 | +.8 | +.8 |
| 9 | 4 | 3.7 | 3.7 | 3.7 | 4 | 2.3 | 2.3 | 2.3 | | | | | 0 | | | |
| 10 | 1 | 2.7 | 2.7 | 2.7 | 3 | 1.5 | 1.5 | 1.5 | | | | | 1 | | | |
| 11 | 0 | 1.9 | 1.9 | 1.9 | 0 | +2.1 | +2.2 | +2.3 | | | | | | | | |
| 12 | 1 | 1.3 | 1.3 | 1.3 | 1 | | | | | | | | | | | |
| 13 | 1 | .9 | .9 | .9 | | | | | | | | | | | | |
| 14 | 0 | | | | | | | | | | | | | | | |
| 15 | 1 | +1.7 | +1.6 | +1.8 | | | | | | | | | | | | |
| 16 | 0 | | | | | | | | | | | | | | | |
| 17 | 1 | | | | | | | | | | | | | | | |
| 18 | 0 | | | | | | | | | | | | | | | |
| 19 | 1 | | | | | | | | | | | | | | | |
| 26 | 1 | | | | | | | | | | | | | | | |
| $P_{\chi^2}$ | | .871 | .890 | .889 | | .978 | .963 | .941 | | .078 | .198 | .287 | | .400 | .337 | .319 |

From the results, indicated by the values of $P_{\chi^2}$, it can be seen that the original empirical distributions were fitted excellently when the estimates of the moments had been thus improved.

The application of the theory to experimental data was continued on the Colorado potato beetle, *Leptinotarsa decemlineata* Say, which lays masses of 20 or 30 eggs. Counts were made on the number of larvae on unit areas of 4 ft. of row of potatoes. Each plot contained 32 such units of which 5 were chosen randomly and examined. There were 2 plots subjected to each of 3 treatments in each block and 7 replications. There

were, accordingly, 3 distributions of 70 observations. The frequency distributions of Neyman's types were again calculated for a number of classes, as shown in table IV, from which it can be seen that the empirical distribution was approached by none of the theoretical. This disagreement was not, however, surprising, for the phenomena under consideration departed widely from Neyman's assumption that the larvae should all be at one stage of development. Since the larvae of *L. decemlineata* ranged from those just hatched to mature, there were superimposed a number of populations each with peculiar values

TABLE IV. *Observations from an experiment on Leptinotarsa decemlineata Say and the fitted distributions of Neyman's Types, A, B and C*

| Class | Treatment 1 | | | | Treatment 2 | | | | Treatment 3 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. |
| 0 | 0 | 7.94 | 4.22 | 3.12 | 20 | 49.20 | 44.54 | 42.49 | 33 | 47.74 | 44.59 | 43.22 |
| 1 | 2 | .00 | .41 | .48 | 11 | .00 | .81 | 1.23 | 12 | .39 | 2.72 | 3.66 |
| 2 | 1 | .00 | .43 | .51 | 6 | .00 | .82 | 1.21 | 5 | 1.08 | 2.78 | 3.42 |
| 3 | 2 | .00 | .45 | .53 | 6 | .00 | .83 | 1.19 | 6 | 2.01 | 2.81 | 3.15 |
| 4 | 0 | .00 | .47 | .56 | 6 | .00 | .83 | 1.17 | 5 | 2.83 | 2.76 | 2.85 |
| 5 | 1 | .00 | .49 | .58 | 1 | .01 | .84 | 1.14 | 0 | 3.19 | 2.62 | 2.53 |
| 6 | 1 | .00 | .51 | .60 | 1 | .02 | .85 | 1.12 | 2 | 3.03 | 2.38 | 2.20 |
| 7 | 0 | .01 | .53 | .63 | 2 | .05 | .86 | 1.10 | 2 | 2.52 | 2.06 | 1.87 |
| 8 | 1 | .02 | .56 | .65 | 3 | .11 | .86 | 1.07 | 2 | 1.92 | 1.71 | 1.56 |
| 9 | 1 | .05 | .58 | .68 | 0 | .21 | .87 | 1.04 | 0 | 1.37 | 1.36 | 1.27 |
| 10 | 1 | .10 | .61 | .70 | 1 | .36 | .88 | 1.02 | 1 | .98 | 1.05 | 1.01 |
| 11 | 0 | .17 | .63 | .72 | 2 | .57 | — | — | 0 | — | — | — |
| 12 | 1 | .29 | .66 | .74 | 1 | .82 | | | 0 | | | |
| 13 | 2 | .45 | .69 | .76 | 1 | 1.09 | | | 0 | | | |
| 14 | 2 | .65 | .71 | .78 | 0 | 1.34 | | | 0 | | | |
| 15 | 0 | .87 | .74 | .80 | 1 | 1.53 | | | 0 | | | |
| 16 | 2 | 1.09 | — | — | 1 | 1.65 | | | 0 | | | |
| 17 | 1 | 1.29 | | | 0 | 1.67 | | | 1 | | | |
| 18 | 0 | 1.44 | | | 2 | 1.60 | | | 0 | | | |
| 19 | 1 | 1.53 | | | 0 | 1.45 | | | 0 | | | |
| 20 | 0 | 1.54 | | | 0 | 1.25 | | | 0 | | | |
| 21 | 1 | 1.47 | | | 1 | — | | | 1 | | | |
| 22 | 0 | 1.35 | | | 0 | | | | | | | the |
| 23 | 0 | 1.19 | | | 0 | | | | | | | with 5 |
| 24 | 0 | 1.02 | | | 0 | | | | | | | |
| 25 | 2 | .84 | | | 0 | | | | | | | values, Γ, |
| 26 | 1 | .69 | | | 0 | | | | | | | ants, it is the |
| 27 | 1 | .58 | | | 1 | | | | | | | information. |
| 28 | 1 | .50 | | | 0 | | | | | | | the quantities, |
| 29 | 1 | .47 | | | 0 | | | | | | | can be obtained |
| 30 | 0 | .48 | | | 0 | | | | | | | only on α being |
| 31 | 0 | .53 | | | 0 | | | | | | | is. For an illus- |
| 32 | 0 | .60 | | | 0 | | | | | | | n Treatment 1, |
| 33 | 1 | .69 | | | 0 | | | | | | | t the respective |
| 34 | 1 | .80 | | | 0 | | | | | | | |
| 35 | 3 | .90 | | | 0 | | | | | | | |
| 36-138 | 39 | — | | | 3 | | | | | | | |

of $\alpha$, $\beta$ and $\Gamma$. Each such population may have been of Neyman's types.

With the composite distributions which must arise when groups are confused, little can be done. It would probably be advantageous in field work to make counts by instar or size, and to treat the distribution for each instar as a separate problem. Such procedure would be advisable for even the customary comparison of survival calculated over all instars, may conceal important phenomena such as differential survival of the instars.

The outstanding characteristic of Neyman's distributions is their bimodality which is well illustrated, for example, in table III under Treatment 1 by both the empirical and theoretical distributions. That such a tendency is common can be seen in the other empirical distributions shown in this paper. It is surprising that this characteristic has not drawn the attention of biological writers, but apparently Neyman first anticipated it on theoretical grounds. The theoretical distributions may have more than 2 modes as can be seen in table IV under Treatment 1, where modes occur for Type A at 0, at 20 and at a value greater than 35; calculations not presented show this third mode to occur at 40. Presumably, these modes represent the occurrence of 0, 1, 2, etc. egg masses in $\Gamma$, the area from which larvae can reach a given unit area.

The preceding work in fitting furnishes us with a comparison of Types A, B and C, when they have the same moments, *i.e.*, the empirical, and permits an indication of their nature under these circumstances. In the cases of the first treatments (tables I and III) where fitted well, the distributions are, much the same, numbered some more fitting of the fitted in table VII where 3 distributions were fitted cases, but best by C, the agreement was not so close. these, however, and for the latter, where the fit was bad

and disagreement of the types great, it is plain that as one goes from Type A, to B and then to C, the expectation for class 0 falls, that for the classes immediately after 0 tends to rise and that for some later classes to fall again. Briefly, the types show progressively less tendency to bimodality.

Having considered the differences between Types A, B and C, when they have the same moments let us now consider how they differ when they correspond to the same values of $\alpha$, $\beta$ and $\Gamma$. First, we know that (6) holds for all types so that $\mu_1'$ will be the same but from (7), (19) and (29), $\mu_2$ will differ. From (6), (7), and (19), the second moment for Type B is greater than that for Type A by $\mu_1'\beta/3\Gamma$ and, similarly, that for Type C greater than that for Type A by $\mu_1'\beta/2\Gamma$.

## THE ESTIMATION OF THE RELATIVE VALUE OF THE BIOLOGICAL CONSTANTS FROM ONE TREATMENT TO ANOTHER

In fitting the distributions of Types A, B and C to the experimental data just discussed, estimates were made of the parameters, $m_1$, $m_2$, $m_1'$, etc., and since these are, as in equations, (1), (2), (14), etc., dependent on the 3 primary biological constants, $\alpha$, $\beta$ and $\Gamma$, estimates of the latter were partially determined. Of the latter, $\alpha$ must have been independent of treatment, that is common to all the distributions arising from a given experiment, but $\beta_i$ and $\Gamma_i$ have been peculiar to the $i$th treatment, and it is possible to estimate their relative magnitude from one treatment to another. Estimates of $\beta_i/\beta_{i'}$ where $i' \neq i$, can, from (6), be obtained as

$$b_i/b_{i'} = \bar{x}_i/\bar{x}_{i'}, \qquad (34)$$

where $\bar{x}$ is the empirical first moment. Similarly, for Type A, from (6) and (7) by the introduction of empirical moments, estimates of $\Gamma_i/\Gamma_{i'}$ can be obtained as

$$g_i/g_{i'} = \bar{x}_i^2(s_{i'}^2 - \bar{x}_{i'})/\bar{x}_{i'}^2(s_i^2 - \bar{x}_i), \qquad (35)$$

where $s^2$ is the empirical second moment. For Types B and C, respectively, (19) and (29) replace (7) but the result is still (35).

The estimates of $\beta_i/\beta_{i'}$ are of general biological interest and are commonly presented in reports on entomological experiments as the survival under the $i$th treatment relative to that under no treatment. Estimates of $\Gamma_i/\Gamma_{i'}$, which are suggested by Neyman's theory are not, of course, ordinarily made, but would indicate how far larvae spread under a given treatment as compared with the distance they spread under, say, no treatment, or one learns to what extent a given treatment disturbed the insects. This study of the effect on dispersion of an insect by an insecticide might profitably supplement the traditional study of the effect on survival in entomological work. Similarly, in ecological work, such dispersion might be of use in a study on an area with respect to colonization by or suitability for an organism.

As an illustration, estimates of the sort just discussed are shown in table V for the data, of tables I and III, on *L. sticticalis* and *P. nubilalis* where the 1st treatment was no treatment, with which all the other treatments were compared. The values of $b_i/b_1$ indicate that moderate kills were effected. Let us consider the values of $g_i/g_1$ in more detail. Since, for *L. sticticalis* the values were greater

TABLE V. *The survival and dispersion of insects under various treatments as compared with the same phenomena under no treatments*

Loxostege sticticalis L.

|  | Tr. 2 | Tr. 3 | Tr. 4 |
|---|---|---|---|
| $b_i/b_1$........ | 0.4 | 0.6 | 0.3 |
| $g_i/g_1$........ | 1.5 | 1.2 | 0.7 |

*Pyrausta nubilalis* Hubn.

|  | Tr. 2 | Tr. 3 | Tr. 4 |
|---|---|---|---|
| $b_i/b_1$........ | 0.8 | 0.4 | 0.4 |
| $g_i/g_1$........ | 1.1 | 0.7 | 0.8 |

than unity for the 2nd and 3rd treatments, apparently the larvae were dispersing more widely under these treatments than under no treatment but, on the other hand, since the value was low for the 4th treatment, which consisted of the 2nd and 3rd in combination, possibly the departures of $g_i/g_1$ from unity were not significant. For *P. nubilalis*, the larvae were apparently dispersed more widely under the 2nd and less widely under the 3rd treatment than under no treatment and for the 4th treatment, which consisted of the 2nd and 3rd in combination, the value was intermediate.

### DIRECT ESTIMATION OF THE DISPERSION OF LARVAE FROM THE CONSIDERATION OF THE MOMENTS OF THEIR DISTRIBUTION

When counts are made on a continuous group of contiguous unit areas, it is possible by combination to secure a new group of larger units. Such groups would yield a series of allied distributions for which both $\alpha$ and $\beta$ would be common and even the various values of $\Gamma$ would be related. The data on *L. sticticalis*, which were introduced in table I and are shown in table VI, satisfy the conditions of continuity and contiguity. Since, however, the plots were 5 units long and 5 wide it is only practicable to combine them into groups of 5 of the first units in one direction or the other. For the $i$th treatment let $\Gamma_{i1}$ be the area of origin of larvae when the smallest units were used, $\Gamma_{i2}$ be the area of origin with 5 units combined in the direction of the rows of beets, and $\Gamma_{i3}$ be the area with 5 units combined crosswise.

We propose to estimate the values, $\Gamma$, on which, of the 3 constants, it is the most difficult to secure information. First, let us estimate the quantities, $\Gamma_{i2}/\Gamma_{i1}$ and $\Gamma_{i3}/\Gamma_{i1}$, which can be obtained as in (35) since it depends only on $\alpha$ being common to 2 distributions. For an illustration, use the data on Treatment 1, when taking into account the respective

size of the two kinds of unit area, we obtain the numerical estimates,

$$g_{12}/g_{11} = 1.973, \qquad (36)$$

$$g_{13}/g_{11} = 2.248. \qquad (37)$$

As is discussed in connection with (35) these estimates are the same whether one starts from Type A, B or C.

Some simplifying assumptions must be made about the nature of the values of $\Gamma$, in order to estimate them explicitly from (36) and (37), so suppose that the larvae

TABLE VI. *Primary data of the insecticidal experiment against Loxostege sticticalis L. by numbers of larvae per unit area*

| Block | Treatment 1 No spray | Treatment 2 Contact insecticide | Treatment 3 Lead arsenate | Treatment 4 Contact spray and lead arsenate |
|---|---|---|---|---|
| 1 | 1 6 1 0 2 | 0 0 0 0 0 | 1 1 2 3 1 | 0 1 0 0 1 |
|   | 0 1 1 2 2 | 0 0 0 1 2 | 3 2 3 1 0 | 1 2 1 2 0 |
|   | 1 1 2 0 0 | 0 0 0 1 2 | 0 1 3 4 0 | 0 0 1 1 1 |
|   | 3 2 3 3 1 | 1 0 0 0 2 | 1 0 0 3 1 | 0 0 0 1 1 |
|   | 6 3 0 3 3 | 0 0 0 0 0 | 1 2 0 3 2 | 2 0 1 0 0 |
| 2 | 0 0 1 0 3 | 1 0 0 0 1 | 0 2 0 0 0 | 0 0 0 0 0 |
|   | 2 0 4 3 0 | 0 2 0 2 0 | 0 1 1 1 0 | 0 0 0 1 0 |
|   | 2 4 1 0 0 | 0 1 2 0 0 | 1 0 0 1 0 | 1 1 0 1 0 |
|   | 1 1 2 0 0 | 0 1 0 1 2 | 0 0 2 0 0 | 1 0 0 2 0 |
|   | 3 1 5 0 1 | 0 1 0 1 0 | 0 0 1 0 0 | 0 0 0 0 2 |
| 3 | 0 0 1 0 0 | 1 0 0 1 2 | 0 0 0 0 2 | 1 0 1 2 1 |
|   | 3 2 0 1 1 | 0 0 0 0 0 | 1 0 0 1 0 | 2 3 0 0 0 |
|   | 1 1 0 0 2 | 0 0 1 2 1 | 4 2 1 1 0 | 1 0 2 2 0 |
|   | 0 5 0 0 0 | 0 0 0 1 1 | 1 2 0 3 1 | 0 1 0 1 0 |
|   | 2 1 0 1 1 | 1 1 0 1 0 | 0 0 0 1 0 | 0 0 0 0 1 |
| 4 | 0 2 0 0 0 | 0 2 0 2 0 | 4 0 0 0 0 | 1 0 0 0 1 |
|   | 1 0 2 0 1 | 1 0 0 0 0 | 1 0 0 0 2 | 1 0 1 1 0 |
|   | 4 0 2 0 1 | 1 0 0 1 0 | 0 0 0 2 0 | 0 0 1 0 0 |
|   | 3 0 1 4 2 | 0 2 2 0 0 | 1 0 0 0 0 | 0 0 1 3 2 |
|   | 3 2 1 2 1 | 1 0 0 0 1 | 0 0 0 2 1 | 0 0 0 0 1 |
| 5 | 0 0 0 0 3 | 0 1 1 0 0 | 3 0 3 1 0 | 1 0 0 0 0 |
|   | 0 1 0 1 0 | 1 0 0 1 0 | 1 0 0 2 1 | 0 0 0 1 0 |
|   | 1 1 0 0 1 | 0 1 1 0 0 | 0 0 0 0 0 | 0 0 0 0 0 |
|   | 0 1 3 0 0 | 1 2 0 0 0 | 0 1 2 0 0 | 0 0 1 0 0 |
|   | 1 0 1 0 0 | 1 0 0 0 0 | 0 1 0 0 0 | 0 0 0 0 0 |
| 6 | 2 0 5 7 2 | 0 1 1 0 0 | 1 1 0 1 0 | 0 0 0 0 2 |
|   | 1 5 2 1 2 | 0 1 0 3 0 | 1 0 2 3 0 | 1 2 0 0 0 |
|   | 1 0 4 0 1 | 0 0 0 0 0 | 2 1 0 2 0 | 0 2 0 1 0 |
|   | 1 3 4 1 4 | 0 0 3 1 0 | 2 0 0 4 4 | 2 1 0 0 1 |
|   | 1 0 0 2 3 | 0 0 0 0 2 | 0 0 0 0 3 | 0 0 1 0 0 |
| 7 | 1 3 4 0 0 | 0 0 0 0 1 | 1 2 2 3 1 | 0 0 0 0 0 |
|   | 1 3 3 3 0 | 1 2 1 1 1 | 1 1 5 0 2 | 0 0 1 1 0 |
|   | 7 9 2 3 1 | 0 0 0 0 3 | 3 3 1 5 0 | 0 0 0 3 0 |
|   | 5 3 1 2 1 | 4 0 1 2 0 | 1 2 0 1 2 | 0 0 1 0 1 |
|   | 4 5 0 0 2 | 0 2 0 0 1 | 0 0 0 3 2 | 0 0 1 0 1 |

TABLE VI (*Continued*)

| Block | Treatment 1 No spray | Treatment 2 Contact insecticide | Treatment 3 Lead arsenate | Treatment 4 Contact spray and lead arsenate |
|---|---|---|---|---|
| 8 | 1 0 0 1 1 | 0 0 0 1 1 | 0 3 1 2 1 | 4 0 0 0 0 |
|   | 0 2 1 2 0 | 0 0 1 0 1 | 1 1 0 2 3 | 0 0 1 0 0 |
|   | 1 5 2 1 0 | 1 1 2 1 0 | 2 2 0 1 0 | 0 0 0 0 1 |
|   | 0 2 1 2 0 | 0 1 1 0 0 | 1 2 0 1 2 | 2 1 0 3 1 |
|   | 1 3 3 3 1 | 0 1 0 0 0 | 1 1 1 0 1 | 1 2 0 0 0 |
| 9 | 4 0 2 3 0 | 0 0 1 0 1 | 0 2 1 0 0 | 0 0 0 0 0 |
|   | 1 2 1 1 2 | 0 0 0 0 0 | 0 1 1 0 0 | 1 0 0 0 0 |
|   | 4 2 0 0 4 | 1 0 0 0 0 | 1 0 0 2 0 | 0 0 0 1 0 |
|   | 1 2 0 0 0 | 0 0 0 1 0 | 0 0 1 3 0 | 0 0 0 0 0 |
|   | 2 3 4 1 1 | 0 1 0 0 0 | 0 1 1 0 0 | 0 0 0 0 0 |
| 10 | 3 0 4 2 0 | 0 0 0 1 1 | 2 2 1 0 0 | 0 0 1 0 0 |
|   | 4 0 4 4 0 | 0 2 2 0 1 | 1 0 2 1 0 | 0 1 0 0 1 |
|   | 0 2 4 1 3 | 1 0 4 0 1 | 0 2 0 0 0 | 1 2 1 0 2 |
|   | 2 0 0 2 3 | 0 1 2 0 0 | 1 2 1 0 1 | 0 1 0 0 1 |
|   | 3 3 4 2 0 | 0 1 0 1 0 | 3 1 1 3 3 | 0 0 0 1 0 |
| 11 | 1 0 3 1 1 | 0 0 0 2 0 | 0 0 0 1 2 | 0 1 0 0 0 |
|   | 1 2 0 0 0 | 0 0 0 2 0 | 1 0 1 1 1 | 0 1 0 0 0 |
|   | 2 1 0 0 3 | 0 3 0 0 2 | 3 3 0 2 0 | 2 0 0 0 0 |
|   | 1 1 1 0 2 | 0 1 0 0 0 | 1 0 0 0 0 | 0 0 1 2 1 |
|   | 0 2 4 2 0 | 0 1 0 0 1 | 1 1 0 0 2 | 0 0 0 3 0 |
| 12 | 1 1 2 1 4 | 1 1 0 2 0 | 0 0 0 0 0 | 0 1 0 1 0 |
|   | 2 2 3 0 1 | 0 0 2 1 0 | 1 2 2 0 0 | 1 0 0 0 0 |
|   | 0 0 0 1 0 | 0 0 1 1 0 | 0 0 1 1 0 | 0 1 0 0 0 |
|   | 1 0 0 0 0 | 0 0 0 2 0 | 1 0 0 2 0 | 0 0 1 0 0 |
|   | 0 1 1 0 1 | 1 2 2 0 1 | 2 1 0 1 0 | 0 2 3 0 0 |
| 13 | 0 1 1 0 0 | 1 0 0 0 0 | 0 0 0 0 0 | 0 0 0 1 0 |
|   | 0 3 3 1 0 | 0 0 0 1 1 | 1 1 0 0 1 | 0 0 0 0 0 |
|   | 0 0 1 0 1 | 0 0 0 0 1 | 0 1 0 1 1 | 0 0 0 0 0 |
|   | 3 1 2 0 1 | 1 0 0 0 1 | 1 0 0 0 0 | 0 0 0 0 0 |
|   | 0 0 0 0 0 | 1 0 0 0 1 | 0 2 0 0 0 | 0 0 0 0 0 |

moved a distance, $x$, across the rows of beets and a distance, $y$, along the rows with equal ease. We can now represent $\Gamma_{i1}$, in figure 1, as a kernel representing the unit area examined and a shell depending on $x$ and $y$. The central unit had been made 36 in., in the direction of the rows, and 22 in. wide, so, in square inches,

$$\Gamma_{i1} = 72x + \pi xy + 44y + 792. \qquad (38)$$

Figures similar to 1 could be drawn for $\Gamma_{i2}$ and $\Gamma_{i3}$ where

$$\Gamma_{i2} = 360x + \pi xy + 44y + 3960, \qquad (39)$$

$$\Gamma_{i3} = 72x + \pi xy + 220y + 3960. \qquad (40)$$

By substituting the right hand side of (38), (39) and (40) into equations (36)

and (37) for the estimates, $g$, we obtained equations which can be solved to estimate that $x = 29.2$ in. and $y = 66.4$ in., for
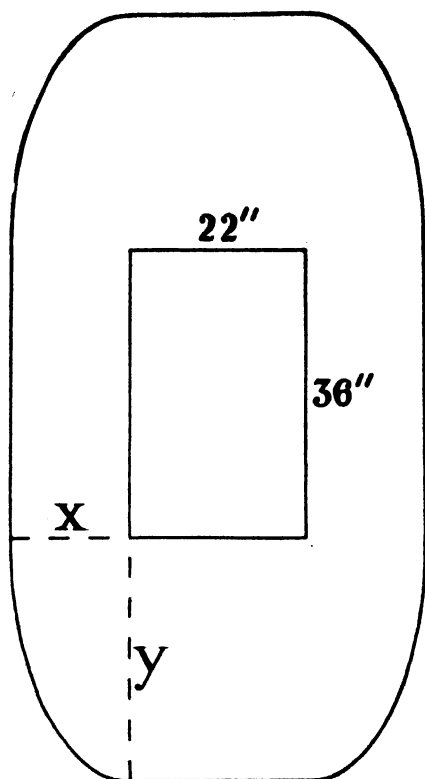


FIG. 1.   The first unit area examined and $\Gamma_n$, the area from which its larvae must have come.

Treatment 1 on *L. sticticalis*. From similar calculations for Treatment 3 we estimated $x = 45.6$ in. and $y = 98.6$ in. Treatment 3 had been sprayed with a contact insecticide which, as an irritant, possibly increased dispersion over that for Treatment 1 which was no treatment. It is perhaps significant that $y > x$, *i.e.*, the movement was estimated to have been greater along the rows than across them. For Treatment 4, we estimated $x = 15.5$ in. and $y = 7.2$ in.   In the case of Treatment 2, it chanced, when the combination of the first unit areas was made in a direction transverse to the rows, that $s^2 < \bar{x}$ and so negative or imaginary values of $x$ and $y$ arose. We can only say, in this case, that $x$ and $y$ were close to zero, as they were for Treatment 4, and such a

conclusion is perhaps reasonable because these 2 sets of plots had been sprayed with an arsenate which might have been expected to depress dispersion.

Having estimated the values, $x$ and $y$, it is possible to estimate from (38), (39) and (40), the values, $\Gamma$, and then, if Type A obtained, from (6) and (7), to estimate $\alpha$ and $\beta$. By the substitution of (19) and (29) for (7), these constants may be obtained from Types B and C. When as in the present case $\Gamma$ is estimated to be the same for all 3 types, $b$ is estimated from Type B to be 3/4 of that from Type A and $a$ from Type B, 4/3 of that from A. Similarly, for Type C, $b$ is 2/3 and $a$, 3/2 of the estimate from A. The exact computations are involved and being made with variable empirical moments, the conclusions are naturally extremely variable, so it is probably unprofitable to pursue the matter further.

THE ESTIMATION OF THE BIOLOGICAL CONSTANTS BY FIELD WORK SUP- PLEMENTARY TO DETERMINING THE DISTRIBUTION OF LARVAE

In the discussion of the preceding section, nothing was known about the biological constants, $\alpha, \beta$ and $\Gamma$, save what could be learned from the moments of the distributions of the larvae. Often, however, it should be possible to count the number of egg masses deposited on an area as well as the number of larvae established so that $\alpha$ and $\beta$ could be estimated directly. Such counts were made during 1936, 1937 and 1938, in the course of studies on the survival of *P. nubilalis*, for which oviposition was followed in early July and counts of larvae were made, on the same area, at the end of August. The counts were made on corn which had been cross-checked, *i.e.*, planted at regular intervals of 42 in. in transverse directions, and later thinned to a single plant at each point of planting. From the direct estimates of $\alpha$ and $\beta$ in conjunction with the moments, dependent on $\alpha$, $\beta$ and $\Gamma$, it should be possible to estimate $\Gamma$ again.

TABLE VII. *Observations on the establishment of Pyrausta nubilalis Hubn. and the fitted distributions of Neyman's types, A, B and C*

| Class | 1936 | | | | 1937 | | | | 1938 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. | Obs. | A Exp. | B Exp. | C Exp. |
| 0 | 24 | 27.4 | 24.9 | 23.8 | 33 | 37.8 | 37.1 | 36.8 | 12 | 15.4 | 13.9 | 13.2 |
| 1 | 6 | 1.4 | 3.9 | 4.8 | 12 | 5.6 | 6.8 | 7.3 | 8 | 3.9 | 5.7 | 6.4 |
| 2 | 4 | 2.8 | 4.0 | 4.5 | 6 | 5.2 | 5.0 | 5.0 | 7 | 5.7 | 6.0 | 6.2 |
| 3 | 5 | 3.9 | 4.0 | 4.1 | 3 | 3.5 | 3.2 | 3.1 | 6 | 6.0 | 5.7 | 5.7 |
| 4 | 3 | 4.2 | 3.7 | 3.7 | 1 | 1.9 | 1.9 | 1.8 | 3 | 5.3 | 5.1 | 5.0 |
| 5 | 2 | 3.8 | 3.3 | 3.2 | 0 | | | | 3 | 4.4 | 4.3 | 4.2 |
| 6 | 1 | 3.0 | 2.8 | 2.6 | 0 | +2.0 | +2.0 | +2.0 | 4 | 3.5 | 3.5 | 3.4 |
| 7 | 1 | 2.3 | 2.2 | 2.1 | 0 | | | | 6 | 2.8 | 2.7 | 2.7 |
| 8 | 2 | 1.7 | 1.8 | 1.7 | 0 | | | | 1 | 2.2 | 2.1 | 2.1 |
| 9 | 1 | 1.3 | 1.4 | 1.3 | 1 | | | | 0 | 1.7 | 1.6 | 1.6 |
| 10 | 2 | 1.0 | 1.0 | 1.0 | | | | | 2 | 1.2 | 1.2 | 1.2 |
| 11 | 3 | .8 | .8 | .8 | | | | | 1 | | | |
| 12 | 1 | .6 | .6 | .6 | | | | | 0 | +2.9 | +3.2 | +3.3 |
| | +1 | +1.8 | +1.6 | +1.8 | | | | | +2 | | | |
| $P_{\chi^2}$ | | .010 | .335 | .528 | | .011 | .064 | .110 | | .080 | .320 | .393 |

In considering these data, it is first necessary to find whether Neyman's distributions gave a satisfactory graduation. To this end the results of fitting, done as in connection with table I, are shown in table VII, with Types A, B and C, against each year. It is apparent from the values of $P_{\chi^2}$ that Neyman's distributions corresponded closely to the observations but that Type A gave the poorest fit, and C the best.

Let us now see for each set of data what magnitude of $\Gamma$ is implied by each distribution when $\alpha$ and $\beta$ are estimated by observations supplementary to those on the distributions. In 1936, when there were 56 plants, 48 egg masses and 167 borers established, we estimated $\alpha$ was 0.857 and $\beta$ was 3.479, when $\bar{x} = 2.982$ and $s^2 = 15.22$; then putting these estimates in (7), for Type A, the estimate of $\Gamma$ was $g = 0.8$. Similarly, for 1937 and 1938 when there were respectively, 56 and 55 plants, 27 and 72 egg masses, with 46 and 201 borers established, we found for both years that $g = 1.0$. Since $\Gamma$ is thus estimated to be of about the same size as the unit area, apparently, no migration occurred. In fact, plants on which egg masses had not occurred harboured some borers so that

migration did occur; hence $\Gamma$ is underestimated. For Type B, $\Gamma$ is estimated from (19) instead of (7) and is 4/3 of the previous estimate and hence somewhat more nearly reasonable. Similarly, for Type C, $\Gamma$ is estimated from (29) instead of (7) and so is 3/2 of the previous estimate. Type C gives the most nearly reasonable estimate of $\Gamma$, as it gives the best fit, but even here, $g$ seems to be unduly small for we should have supposed that the area from which larvae could reach a unit area would be several times greater than the unit and so $g$ would be at least 2 or 3.

When Types A, B and C are given the same values for the first 2 moments, if, as in the present section, $\alpha$ is assumed to be the same for all types then so is $\beta$, since (6) is common, and $\mu_2$ is made the same by differences in $\Gamma$; if, on the other hand as in the preceding section, $\Gamma$ is assumed the same, both $\alpha$ and $\beta$ must differ.

Let us consider what these estimates of $\Gamma$ mean in concrete terms of distances the larvae moved. If we introduce certain simplifying assumptions, after the manner of the preceding section, and say that the larvae can move a distance of, $x = y$, in any direction in the field with equal ease, then a picture similar to figure

1 can be built up. Thus, consider the estimate, $g = 1.332$, from Type B for the data of 1937, when we estimate $x = 3.3$ in., which is indeed a short distance.

It will be noticed that the work of this section and of the preceding section, leads by different methods to estimates of $\Gamma$ and thereby to estimates of the other biological constants. Unfortunately, however, for neither section are the data such that both methods are applicable. With data suitable for both procedures a more thorough investigation of Neyman's types might be made, for we could judge them from the consistency of the 2 sets of estimates of the biological constants.

The information on oviposition permits us to see whether our data conform to one of Neyman's assumptions, namely that the egg masses were laid in a purely random manner. In this work, the number of egg masses laid in each unit area had been recorded so that it was possible to prepare the frequency distributions shown in table VIII for each year

TABLE VIII. *The distribution of egg masses per unit area from survival studies on Pyrausta nubilalis and the fitted Poisson distributions*

| Class | 1936 | | 1937 | | 1938 | |
|---|---|---|---|---|---|---|
| | Obs. | Exp. | Obs. | Exp. | Obs. | Exp. |
| 0 | 26 | 23.8 | 37 | 34.6 | 14 | 14.9 |
| 1 | 19 | 20.4 | 14 | 16.7 | 21 | 19.4 |
| 2 | 7 | 8.7 | 2 | 4.0 | 11 | 12.7 |
| 3 | 1 | 2.5 | 3 | .6 | 7 | 5.6 |
| 4 | 3 | .5 | | .1 | 2 | 1.8 |
| 5 | | .1 | | | | .5 |
| 6 | | | | | | .1 |
| $P_{\chi^2}$ | .649 | | .430 | | .788 | |

and to fit for each a Poisson distribution with the same mean. As can be seen, the agreement was good, hence the oviposition was practically random. Such agreement cannot be expected in all experiments so that we must face the question of how the theoretical distributions would be modified and how they would fit if the oviposition had not been random. Further studies on this problem will be necessary in order for field workers to be able to use Neyman's theory with confidence.

## THE APPLICABILITY OF THE DISTRIBUTIONS OF PÓLYA

Prior to the work of Neyman ('39), Pólya ('31) had suggested two possible contagious distributions and it will be instructive to apply these in the present work. The first of these distributions may be designated, Type 1, where

$$P\{X = n\} = \frac{1}{n!}\frac{d^n}{du^n}\{1 - (u - 1)m_1\}^{-m_2}\Big]_{u=0}, \quad (41)$$

from which, conveniently,

$$P\{X = n+1\} = \frac{m_1(m_2 + n)}{(n+1)(m_1+1)} P\{X = n\} \quad (42)$$

and the second, Type 2, where

$$P\{X = n\} = \frac{1}{n!}\frac{d^n}{du^n} e^{\frac{2m_1m_2(u-1)}{2+m_1-m_1u}}\Big]_{u=0}. \quad (43)$$

For the distributions given by both (41) and (43), (8) and (9) hold, so that the parameters can be estimated as in (10) and (11).

The two distributions of Pólya were fitted with the results, shown in table IX, to data on *L. sticticalis, P. nubilalis* and *L. decemlineata.* The fit to the data on *L. sticticalis* was bad for each distribution and it is hard to conjecture why the theory should have failed for this homogeneous material unless it does not, generally, represent such entomological data. The correspondence with the data on *P. nubilalis* was best but even there apparently the theoretical distributions were unimodal and the first two empirical seem to have been bimodal; the fit possibly does not test as bad because the differences between the theoretical and empirical distributions happened not to be of the magnitude of the chance errors. In the case of *L. decemlineata*, Pólya's distributions fitted no better than those tried earlier. Generally, the impression

TABLE IX. *The applicability of Pólya's distributions to the data from 3 entomological experiments*

| Class | Treatment 1 | | | Treatment 2 | | | Treatment 3 | | | Treatment 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | 1 Exp. | 2 Exp. | Obs. | 1 Exp. | 2 Exp. | Obs. | 1 Exp. | 2 Exp. | Obs. | 1 Exp. | 2 Exp. |
| *Loxostege sticticalis* L. (as in table I) | | | | | | | | | | | | |
| 0 | 117 | 153.2 | 164.6 | 205 | 259.2 | 267.7 | 162 | 212.6 | 223.2 | 227 | 253.6 | 257.9 |
| 1 | 87 | 68.9 | 54.4 | 84 | 31.1 | 20.0 | 88 | 51.2 | 37.0 | 70 | 40.7 | 33.4 |
| 2 | 50 | 38.9 | 36.8 | 30 | 13.7 | 13.0 | 45 | 24.5 | 23.7 | 21 | 15.7 | 16.9 |
| 3 | 38 | 23.4 | 24.6 | 4 | 7.5 | 8.5 | 23 | 13.7 | 15.2 | 6 | 7.2 | 8.4 |
| 4 | 21 | 14.5 | 16.1 | 2 | 4.5 | 5.5 | 5 | 8.2 | 9.6 | 1 | 3.6 | 4.2 |
| 5 | 7 | 9.2 | 10.4 | | | 3.6 | 2 | 5.1 | 6.1 | | | |
| 6 | 2 | 5.9 | 6.7 | | +9.0 | | | | 3.8 | | +4.2 | +4.2 |
| 7 | 2 | 3.8 | 4.2 | | | +6.7 | | +9.7 | | | | |
| 8 | 0 | | | | | | | | +6.4 | | | |
| 9 | 1 | +7.2 | +7.2 | | | | | | | | | |
| *Pyrausta nubilalis* Hubn. (as in table III) | | | | | | | | | | | | |
| 0 | 19 | 13.7 | 16.5 | 24 | 22.2 | 26.2 | 43 | 46.0 | 48.3 | 47 | 50.2 | 53.3 |
| 1 | 12 | 18.4 | 16.8 | 16 | 22.3 | 19.2 | 35 | 30.1 | 26.9 | 23 | 28.3 | 24.2 |
| 2 | 18 | 18.3 | 16.8 | 16 | 18.8 | 17.0 | 17 | 18.3 | 17.9 | 27 | 16.6 | 16.2 |
| 3 | 18 | 16.1 | 15.2 | 18 | 14.8 | 14.2 | 11 | 10.8 | 11.2 | 9 | 9.9 | 10.4 |
| 4 | 11 | 13.3 | 13.0 | 15 | 11.3 | 11.3 | 5 | 6.3 | 6.7 | 7 | 5.9 | 6.5 |
| 5 | 12 | 10.5 | 10.6 | 9 | 8.4 | 8.8 | 4 | 3.6 | 3.9 | 3 | 3.6 | 3.9 |
| 6 | 7 | 8.0 | 8.3 | 6 | 6.2 | 6.6 | 1 | ⎰ 2.1 | ⎰ 2.2 | 1 | ⎰ 2.2 | ⎰ 2.3 |
| 7 | 8 | 6.0 | 6.4 | 5 | 4.5 | 4.9 | 2 | { 1.2 | { 1.2 | 1 | { 1.3 | { 1.4 |
| 8 | 4 | 4.5 | 4.8 | 3 | ⎰ 3.3 | ⎰ 3.6 | 2 | | | 0 | | |
| 9 | 4 | ⎰ 3.3 | ⎰ 3.5 | 4 | 2.4 | 2.6 | | ⎱ +1.6 | ⎱ +1.7 | 0 | ⎱ +2.0 | ⎱ +1.8 |
| 10 | 1 | { 2.4 | { 2.5 | 3 | 1.7 | 1.8 | | | | 1 | | |
| 11 | 0 | ⎱ 1.7 | | 0 | | | | | | 1 | | |
| 12 | 1 | | | 1 | ⎱ +4.1 | ⎱ +3.8 | | | | | | |
| | +5 | ⎱ +3.8 | +5.6 | | | | | | | | | |
| $P_{\chi^2}$ | | .581 | .874 | | .635 | .819 | | .839 | .481 | | .076 | .066 |
| *Leptinotarsa decemlineata* Say (as in table IV) | | | | | | | | | | | | |
| 0 | 0 | .00 | .00 | 20 | .39 | .40 | 33 | 11.42 | 11.60 | | | |
| 1 | 2 | .00 | .00 | 11 | 1.73 | 1.76 | 12 | 17.68 | 17.49 | | | |
| 2 | 1 | .00 | .00 | 6 | 4.11 | 4.13 | 5 | 16.13 | 16.01 | | | |
| 3 | 2 | .00 | .00 | 6 | 6.87 | 6.85 | 6 | 11.31 | 11.33 | | | |
| 4 | 0 | .00 | .00 | 6 | 9.05 | 9.01 | 5 | 6.73 | 6.80 | | | |
| 5 | 1 | .00 | .00 | 1 | 10.01 | 9.97 | 0 | 3.58 | 3.63 | | | |
| 6 | 1 | .00 | .00 | 1 | 9.67 | 9.65 | 2 | 1.75 | 1.77 | | | |
| 7 | 0 | .00 | .00 | 2 | 8.36 | 8.37 | 2 | .80 | .80 | | | |
| 8 | 1 | .00 | .00 | 3 | 6.60 | 6.62 | 2 | .35 | .34 | | | |
| 9 | 1 | .00 | .00 | 0 | 4.82 | 4.85 | 0 | .15 | .14 | | | |
| 10 | 1 | .00 | .00 | 1 | 3.29 | 3.31 | 1 | .06 | .05 | | | |
| 11 | 0 | .00 | .00 | 2 | 2.12 | | 0 | .02 | | | | |
| 12 | 1 | .01 | .00 | 1 | 1.30 | +5.08 | 0 | .01 | +.04 | | | |
| 13 | 2 | .02 | .00 | 1 | .76 | | 0 | .01 | | | | |
| | +57 | +69.97 | +70.00 | +9 | +.92 | | +2 | | | | | |

given by table IX is that Pólya's distributions do not correspond to the data under consideration, particularly in that they do not have the necessary tendency to bimodality.

## SUMMARY

Neyman's contagious distribution of Types, A, B and C, with 2 parameters, depending on the biological factors of numbers of egg masses deposited, sur-

vival of larvae and the dispersion of larvae, all fitted excellently 8 observed distributions of larval insects per unit area in 2 experiments on fairly homogeneous populations. In addition, for 3 distributions from life-history work all 3 types fitted well but Type C the best. It appears that the theory of Neyman may prove generally applicable to such data. Neyman's distributions are often bimodal and apparently correspond to the data; yet it appears that biologists had never remarked on this bimodality before it was anticipated by Neyman. For 3 further distributions from an experiment, on larvae which were of various ages, the fit was generally bad. Probably, in such work, the counts should be made by instar or size because the survival of the larvae, of which the comparison is the main purpose of such experiments, must vary from one instar to another. It was pointed out that the relationship between moments of a distribution leads to an estimate of the relative extent to which larvae are stimulated to disperse, say by spraying, as well as the established estimate of the relative extent to which they survive under treatment. By appropriate arrangement of the field work one can estimate the actual distances that larvae have moved.

Two types of general contagious distributions developed by Pólya fitted one set of empirical distributions from entomological field work but not another of which the data were homogeneous.

## DISCUSSION

The present study on the frequency distribution of larval insects arose from discussions between Professor Neyman and the writer on the problem of testing the results from entomological experiments in the field. Professor Neyman built up his theory ('39) to provide for such distributions a general model which has been found in the present paper to agree well with data. The theory relates the

distribution of insects to their survival and their dispersion. It is hoped that this work will lead to the development of statistical criteria for testing the significance of the variation with treatment in this survival and dispersion.

Although Professor Neyman built his theory on an assumed machinery governing the movement of larvae, he also produced evidence that his theory fitted very well some data on the distribution of yeast cells in a haemacytometer. As he says (pp. 36 and 37), the machinery governing the distribution of the yeast cells is not so clear as in the case of insects but possibly the position of one cell influences that of another and so the distribution is contagious. The fact, however, that the theory fitted data, other than entomological, suggests that it possibly is applicable to a wide range of data. It is possible, for example, that experience will show the theory to fit data such as those on a plant colonizing an area or on the distribution of a gregarious animal. In some cases the constants involved may have the same physical meaning as in the present study, but in some the physical meaning may be obscure. It is hoped that the present paper may point the way to studying contagious distributions in other fields, for the contagious distribution where the occurrence of organisms is not independent, as is so often discussed under the term of association, is one of the fundamental problems of ecology although little attempt has been made to assess the magnitude of the effects involved.

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# POLYGONAL GRAPHING OF ECOLOGICAL DATA

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## THE ECOLOGICAL PROBLEM OF FACTOR COMPLEXES

The complexity of the many, variable and interacting factors contributing to the effective environment of particular plant or animal species or associations has been recognized by ecologists generally. Clements ('28) states: "Every habitat is a complex in which the factors are almost inextricably interwoven. Each factor influences every other factor and is in turn affected by it. This relation should never be lost sight of since it is essential to the proper understanding of every factor indicator. This is particularly true of the direct factors: water, temperature, light, solutes, and soil oxygen." Similarly, in Fuller and Conard's translation of Braun-Blanquet ('32) this situation is emphasized: "The impossibility of separating the various factors that are operative in nature greatly hampers the study of synecology. We must not, however, overlook the fact that in nature we always meet, not a single factor but a whole complex of them. These inter-relations of factors have received little synecological consideration although they offer a rich field of investigation." Weaver and Clements ('29) add: "All formations are limited by climate—by a particular climatic complex. Distance from the ocean, differences in latitude and altitude, etc., all profoundly affect precipitation and temperature as well as other climatic factors." Hess, as translated and edited by Allee and Schmidt ('36), notes that the complex includes even more variables in animal ecology: "Among plants the relations with the total environment are much more direct and obvious than among animals. The capacity for motion makes animals to a degree independent of their environment." That the solution of this situation requires a many-sided approach is summarized by Lundegardh ('31): "The aim of experimental ecology is the investigation of the plant's (or animal's) reaction to a certain 'constellation' of ecological factors with a view to discovering how the plant (or animal) behaves in its natural habitat. There exists no sharp distinction between this study and synecology, which investigates plant (or animal) societies in the same way."

In a summary account of the "Prairie Peninsula" of Central North America, Transeau ('35) recognizes that the complexity of the ecological habitat is accentuated by the necessity of interpreting its position in a series: "Any proposed explanation emphasizing a single factor or group of factors that does not take into account past climates, the soil types preceding the development of prairyerths must fall far short of solving the complex problems surrounding this unique ecological formation." The complexity of the precipitation factor is illustrated by graphs, or "precipitation patterns," throughout the year, the variability from year to year accentuating the problem of evaluation.

## METHODS OF SOLVING THE ECOLOGICAL COMPLEX

Various methods of solving the inter-relationships between the organism and the environment, whether causal or parallel, have been devised.

*By the control of factors, with one variable only.*—"The reason why the plant physiologist hesitated so long before attacking ecological problems is quite clear. The living organism displays so many simultaneous processes that it is impossible to follow them all at once. Accordingly there is in plant physiology a standard rule for experimental work which must be followed. The organism must be brought under constant conditions and

that factor alone varied whose influence is to be studied," Lundegardh ('31). It is conceded by the same author: "The fact that we still know relatively little about the causal relationship between environment and vegetation is scant reason to deny the existence of such a relationship. When a plant is brought into the laboratory for experiment, it is removed from its natural environment into a simplified environment and perhaps upset altogether; and in the end nothing may be known of the part played in the natural life of the plant by the phenomena measured in the laboratory."

*Establishment of definite laws.*—To quote, Hess ('37), "In contrast to the situation in historical zoogeography, ecological zoogeography bears the germs of a truly causal science. Although it is still in its infancy, some general laws have already been established such as the application of the law of minima to the phenomena of distribution, Bergmann's rule and the correlation between the weight of the heart and the isotherms of climate." We may add, the formulae for the rate of growth. Liebig's "Law of the Minimum" is often known as the "Principle of Limiting Factors." "Liebig found that in the growth of plants the food element which is least plentiful, in proportion to the plants' needs, limits their growth. Light and oxygen are wanting at relatively few places but temperature, humidity, and water supply vary in a much greater degree; and these factors accordingly are the most important causes of variation in animal distribution. In other words the selection of the animals in a given environment is determined by the habitat factor which most nearly approaches the minimum. The closer a single factor approaches the limiting value the fewer is the number of species in the situation in question" (Hess, '37). Lundegardh ('31) draws attention to the limitations of this method: "But when no factor is clearly in minimum the investigator has to be perfectly clear as to the significance of the law of relative effects."

*By the establishment of ecological valences and by using ecological indicators as standards.*—The use of ecological indicators as standards, and the establishment of ecological valence recognizes standards which measure only within the range of biotic tolerance. As expressed by Hess, Allee, and Schmidt: "The amplitude of the range of the conditions of life within which an animal (or plant) is able to exist may be designated as the ecological valence." Weaver and Clements ('29) state that: "In delimiting climates and climaxes, the plant is the ultimate criterion, and climatic measurements must be interpreted in terms of plant growth." On the other hand, "the difficulty of drawing exact boundaries between formations may be appreciated when it is realized that developmental studies have not yet determined whether or not all the climatic areas are actually occupied by the type of vegetation which they may ultimately support." Braun-Blanquet ('32) recognizes the same limitations of this method when he criticizes as "at the same time too narrow and too broad" the definition of Flahault and Schröter ('10) for an "association," which is designated as a "plant' community of definite floristic composition, presenting a uniform physiognomy and growing in uniform habitat conditions."

*By the method of parallel graphs.*—Physiologists have frequently represented data for processes which are coincident, parallel, or in immediate series by the method of parallel graphs, each graph showing the relationship between two expressions. For instance, Briggs and Shantz ('16) plot transpiration of oats against time for one day, together with the parallel graphs for the factors, air, temperature, psychrometer readings, transpiration, and wind velocity against "time." Correlation coefficients may be determined. In this case the correlation coefficient of transpiration and radiant energy is 0.66 to 0.75 and the temperature and humidity curves are nearly parallel while wind shows the least correlation.

Lundegardh ('31) comments that: "The significance of this parallelism is uncertain. The work of Briggs and Shantz was carried out under 'ideal' conditions especially as regards the water content of the soil. In nature, however, the water content varies continuously and the work of Livingston and Hawkins and of Maximov and Lebedincev ('23) and Ilgin ('22) shows that at the time of greatest transpiration there is a temporary water deficit in the soil. Under these conditions stomatal regulation comes into play and the normal course of transpiration is markedly altered."

One of the most extensive and noteworthy contributions to the exact study of the relation between climatic factors and the distribution of vegetation areas has been presented by Livingston and Shreve ('21). In addition to charts showing vegetation, temperature, precipitation, humidity, evaporation, moisture ratios, wind, sunshine, temperature summation, and moisture-temperature ratios, with sub-factors, there are given numerous parallel graphs representing the same factors. The significance of these graphs is interpreted. The account in this paper uses the same data, and presents it in the form of polygonal graphs with the hope that the value of Livingston and Shreve's data may be increased by another method of orientation.

## POLYGONAL GRAPHING

Polygonal graphing presents several of the various factors constituting the complex of variables known as the environment or habitat in the form of a unit, which is represented by a polygon or polygons. The form, and degree of symmetry of the polygon designates the habitat characteristics.

### 1. Construction of the Standard Scale (fig. 1)

The general scheme with descriptions was presented in an earlier paper (Hutchinson, '36).

*Selection of factors.*—Since each factor is represented as units on a radius, the number of factors which may be represented is theoretically unlimited; in practice, however, it is not feasible to graph more than ten variables in any figure. Factors which are most significant in relation to the biotic limits of the group or association are selected. Of those recorded by Livingston and Shreve the following, which apply to the frostless season, seem most appropriate: daily mean precipitation in inches (Mn.P.); the days of rain, over 0.1 inches for any day (D.R.); the evaporation, as the daily mean in inches (E.); the relative humidity (H.); the hours of sunlight (H.Sun.); the physiological summation of temperature $(\Sigma T)$; the days in the frostless season (D.F.S.); and the physiological value which is the product of the physiological temperature summation by the precipitation by the reciprocal of evaporation $(PT/E)$.

*The grouping of factors.*—The sub-factors of a major factor are co-oriented on adjacent radii; the primary factors used are: water supply, evaporation (water loss), light, temperature, and physiological value. Since relative humidity is related to both water supply and evaporation it has an intermediate position graphically; similarly, the factor days in the frostless season is located between temperature summation and hours of sunlight.

*Individual scales for factors.*—The outer four-fifths of each radius is used as a scale radius. The terminal points of the scale-radii are given the maximal and minimal values represented in the data available, and ideally should represent all known values. The equal radii are divided into suitable gradations. Consequently co-incident variations or values represented on the graphs are relative to the maximum range in each case and since this is represented by similar radii, factors are reduced to a common denominator expressed as radius distance.

As indicated on the graph (fig. 1) the maxima and minima, during the frostless season, for the respective factors are: evaporation, daily mean in inches, 0.05, 0.35; relative humidity, 22, 88; precipitation, daily mean in inches, 0.01, 0.20; days of rain, more than 0.1 inches, 0, 300; hours of sunlight, in hundreds, 11, 30; days in the frostless season, 25, 365; physiological temperature summation, in



Climatic Factors Scale    Frostless Season
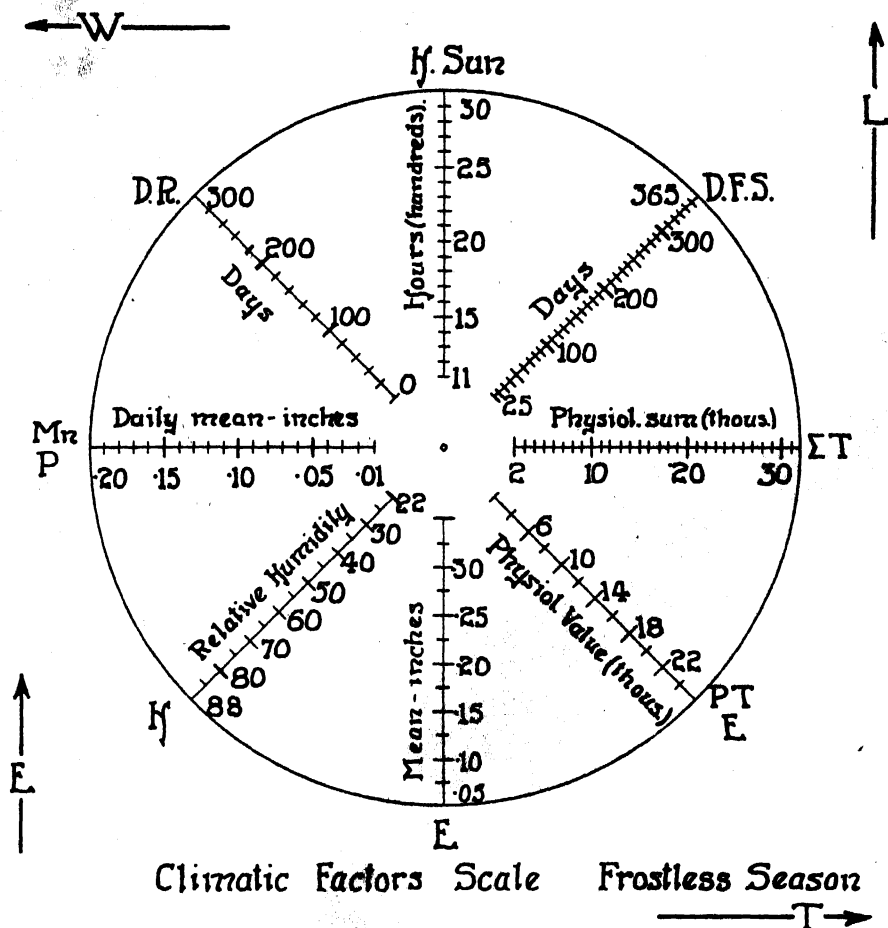
FIG. 1. Climatic Factors Scale. Extremes of radii indicate maxima and minima for the several factors, including all data recorded by Livingston and Shreve for the United States. All factors, with the exception of evaporation, have a general, direct (positive) effect upon plant growth and are shown as increasing numerically toward the circumference; evaporation has an inverse (negative) effect and reads numerically toward the center.

H. Sun.—the number, in hundreds, hours of sunlight during the frostless season (1,100 to 3,000).

D.F.S.—number of days in the frostless season (25–365).

$\Sigma$T.—summation of physiological temperature; Livingston's summation of the indices of temperature efficiency of plant growth for the days of the frostless season (2,000 to 32,000).

PT/E.—the product of the mean daily precipitation by the physiological temperature summation divided by the mean daily evaporation, all for the frostless season (2,000 to 26,000).

E.—mean daily evaporation in inches, for the frostless season (.05–.35 inches).

H.—mean daily relative humidity for the frostless season (22–88).

Mn.P.—mean daily precipitation in inches for the frostless season (.01–.20).

D.R.—number of days in the longest rainy season (0–300).

thousands, 2, 32, and physiological value in thousands, $PT/E$, 2, 24.

*Positive and negative factors.*—Factors are divided into two classes, positive and negative according to their effects. In this case the effect upon growth is the primary consideration for determining the sign. If increased numerical values of the factor are accompanied by increase in growth, at least up to an optimum value, that factor is denoted as positive; negative factors have the reverse effect. In this instance, evaporation is the only negative factor. Positive factors have minimal values placed at the inner extremity of the scale-radius while negative factors have minimal values at the outer extremity.

*General arrangement of readings.*— Sunlight values increase outward and upward; evaporation values inward and upward; precipitation values outward, to the left, and temperature values outward, to the right. The position and direction of the arrows indicate these directional value gradations (fig. 1).

## 2. The Charting of Data (figs. 2, 3)

The minimal values for each factor of a definite climatic complex, that is for a given position and time, are located as points on their respective radii and these points are connected to form a polygon, here an octagon. This figure represents graphically the minimal features of the climatic complex. It follows from the above that minimal values for negative factors have a high numerical index.

Similarly, maximal values of a definite climatic complex are plotted and charted by joining the points representing the respective values for that time and place.

Median points, between the extremes, are measured and these points are joined.

The figure delimited by the inner and the outer polygons represents the range of the particular climatic complex, and may be known as a *bio-climatic zone*. The median polygon represents a climatic complex which approaches the optimum

of the zone, and may be called a *bio-climatic median*.

## 3. Interpretation of Polygons

The data represented in figures 2 and 3 are for values reported by Livingston and Shreve ('21) for the principal vegetation areas of the United States, namely: the deciduous forest (fig. 2.**A**.); the grassland deciduous forest transition (fig. 2.**B**.); the northern mesophytic evergreen forest of the east (fig. 2.**C**.); the southeastern evergreen forest (fig. 2.**D**.); the grassland (fig. 3.**A**.); the desert (fig. 3.**B**.); the northern mesophytic evergreen forest of the west (fig. 3.**C**.); and the hygrophytic forest (fig. 3.**D**.).

*Symmetry and balance.*—The degree of symmetry of the polygon is an expression of the balance of the factor complex. The median polygons generally show a more nearly balanced habitat than the minimal or the maximal polygons. Provided the standard scale has been constructed in accord with the conditions indicated above, the degree of symmetry is an expression of the total conformity to biotic requirements.

The most marked symmetry is evident in the southeastern evergreen forest (fig. 2.**D**.) and this applies to the polygons representing minimal, maximal, and median values of the climatic complex. The climates of the eastern area (fig. 2.**A**–**D**.) are more balanced than those of the west with the exception of the grasslands (fig. 3.**A**.). The graphs for the desert, northern mesophytic evergreen forest of the west and the western hygrophytic forest show marked asymmetrical features (fig. 3.**B**–**D**.).

*Asymmetrical contour and biotic deficiencies or advantages.*—Variations from the regular polygon may indicate irregularities in the biotic environment and may be shown as extensions or depressions, that is as abnormally high or low values for any one factor or set of factors in the environmental complex. The climatic conditions for the regions of forest shown in the graphs all have an extension

of the polygon indicating high humidity accompanied by low evaporation values (fig. 2.A–D. and fig. 3.C, D.). This feature is most marked in the cases of the northern mesophytic evergreen forest of the east and west, and of the western hygrophytic forest (figs. 2.C. and 3.C, D.). The climate of the northern mesophytic forest of the east is notably deficient in sunlight and temperature (fig. 2.C.); the northern mesophytic forest of the west in precipitation and temperature summation

(fig. 3.C.); and the hygrophytic forest in sunlight and temperature summation (fig. 3.D.). The climatic complex of the desert is abnormally deficient in the number of days of rain and in the physiological value $PT/E$ while at its minimal climatic extremes, there is deficiency in all factors represented except hours of sunlight, which are intermediate in value.

*The biotic tolerance and the climatic range as represented by polygons* (figs. 2 and 3). The range of biotic tolerance
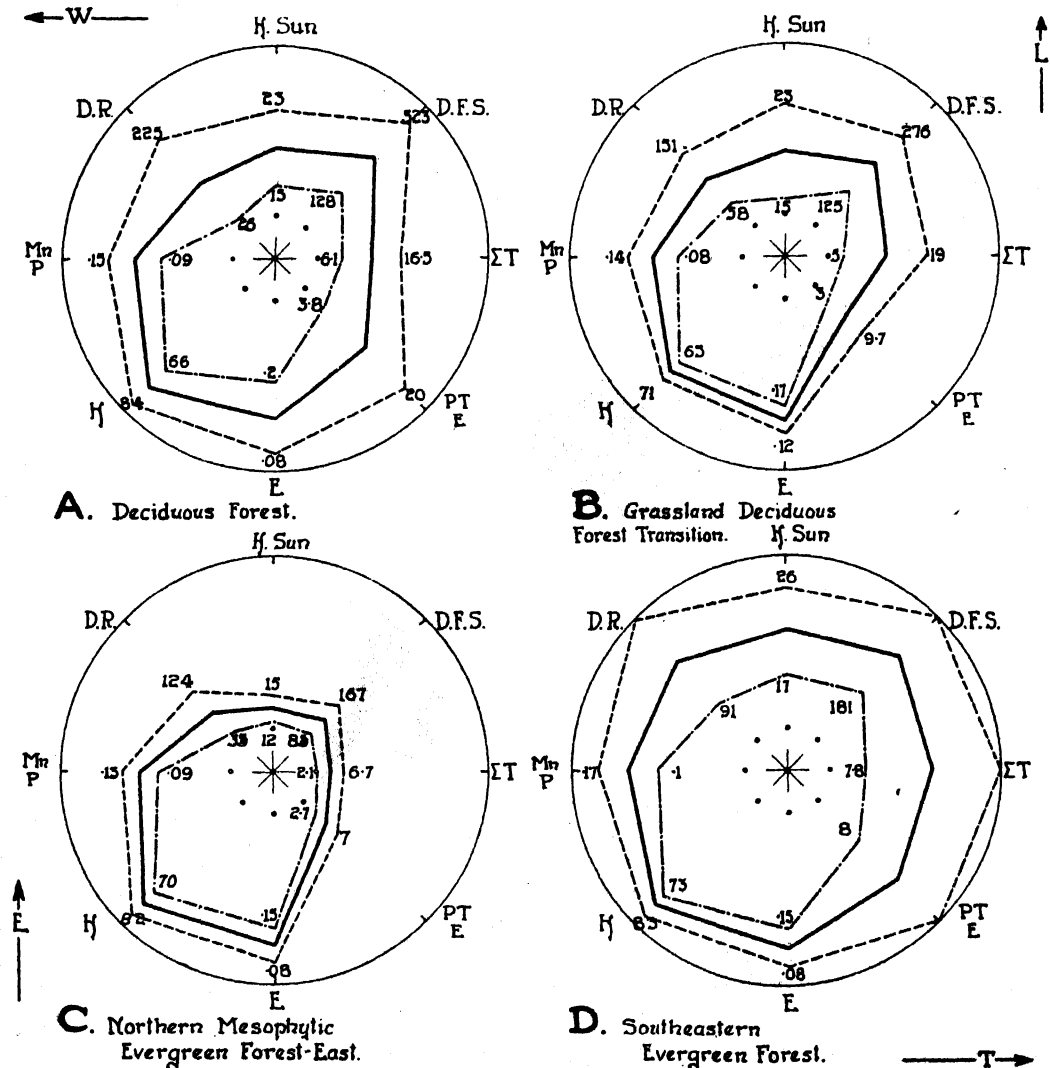


FIG. 2. Polygonal graphs representing, in each case, the bio-climatic extremes, and median, which characterize the following vegetation regions; the values and factors have reference to the key scale, figure 1.

A. Bio-climatic graphs for the deciduous forest; B. for the grassland deciduous forest; C. for the northern mesophytic evergreen forest, east; D. the southeastern evergreen forest.

A. Grassland.

B. Desert.

C. Northern Mesophytic Evergreen Forest-West

D. Hygrophytic Forest
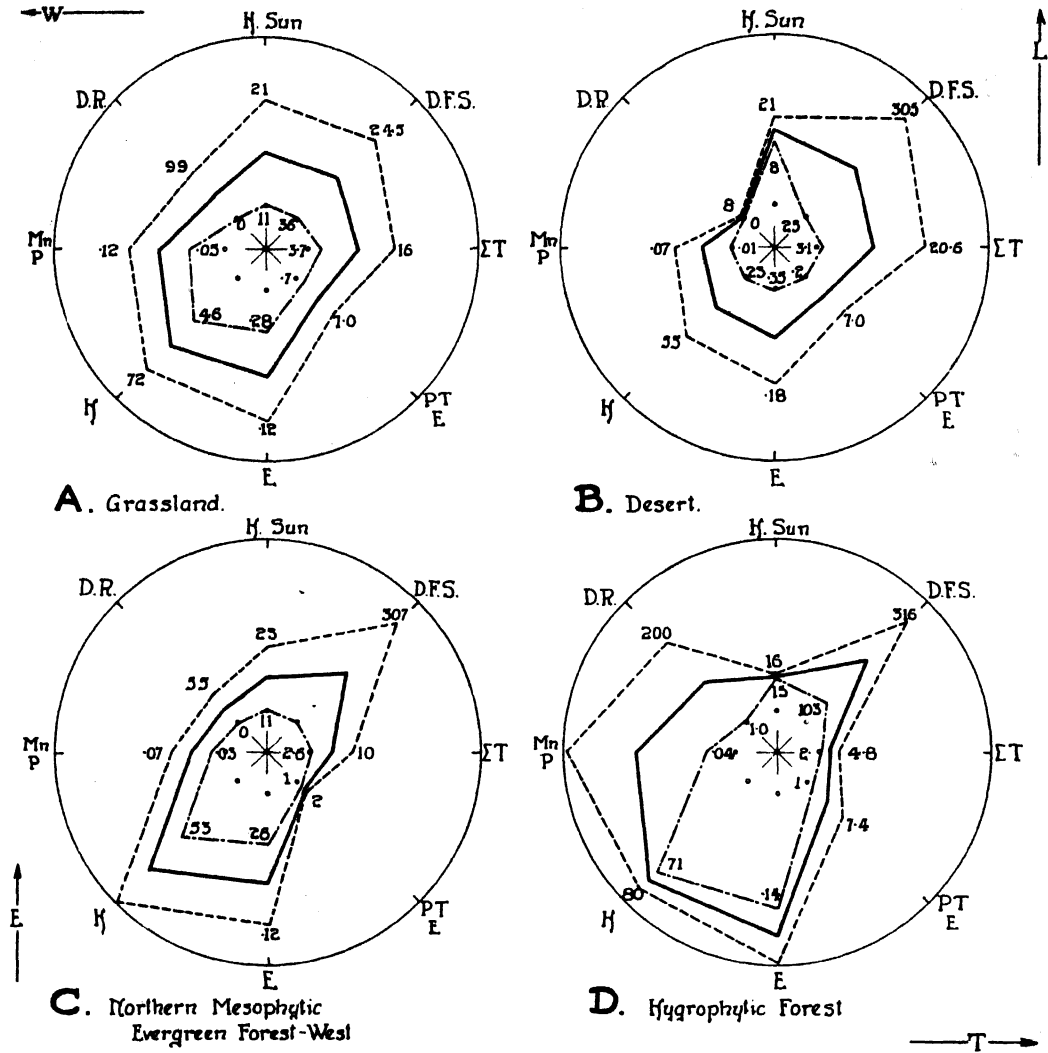
FIG. 3. Polygonal graphs representing the bio-climatic extremes, and median, which characterize the vegetation regions (cf. plate 1 for key chart).

A. Bio-climatic graphs for the grasslands of United States; B. for the desert; C. the northern mesophytic evergreen forest; and D. for the western hygrophytic forest.

toward the climatic factors varies greatly and is readily illustrated by the distances between the inner and outer polygons representing the minimal and the maximal factor values of the habitat. The climatic ranges of the southeastern evergreen forest (fig. 2.D.) and of the deciduous forest (fig. 2.A.) are great, except for the factors of humidity and evaporation. The general climatic range of the northern mesophytic forest of the east is limited generally (fig. 2.C.) while the range of the desert is notably re-

stricted toward days of rai̶ally located ); the northern mesophytic e̶atic zones, est of the west is similarly to humidity the physiological value $PT$/ one with respect phytic forest, in both and the hypo-zone and temperature sum̶nt, temperature and ̶ation factors (fig.

BIO-CLIMATIC ZON
Po
c forest median is very
1. The Desir f the northeastern meso-
ccept that the days of the
As early as ̶n characteristic is in the
chaos in ̶ng. 4.C.).

classification and a committee was appointed to report on the matter at the Botanical Congress. Again in 1913 Shelfold states: "Terminology in ecology is still unsettled and changing." In 1920 Tansley noted: "The opinions and practices of synecologists in regard to the classification of vegetation appear superficially to be at least as great a confusion today as twenty years ago." "The widely varying opinions of the authors are due in the first place to their varying preoccupation." Several initial or primary interests are cited, such as floristics, habitats, life forms, topography and organic entities; these have given varied directions to the ecological perspective.

Recognition of these difficulties has not decreased the recent variety in systems of ecological classification. A few examples may be cited.

## 2. *Various Recent Systems of Ecological Classification*

*Geographical, or physiographic.*—Pliny classified animals as Aquatilia, Terrestria, and Volatilia and for many this is still the primary basis. Braun-Blanquet ('32) uses a combination of this system and the phylogenetic series of plants in formulating an ecological system while Hess ('37) sub-divides the water and ·l forms to produce a physiographic n.

/ *basis of life-forms.*—As annuals, perennials, adopted by Pound ₁₃/ts; Drude; and as developed anquet ('32) secondarily to liographic divisions. Simi- 'e's ('31) tundra province nce emphasize life-form

habitat factors.—"The en to include every- factors operative in te locality so far as plants" (or ani-Warming ('09) ially the water classified life asis of tem-

C. Northern Me. Evergreen Fo.

Fig. 2. Polygonal gi dian, which characterize the to the key scale, figure 1.

A. Bio-climatic graphs C. for the northern mesophytic

*perature;* while many others and especially Livingston and Shreve ('21) have used the *water* factor as a primary factor in conjunction with vegetational grouping. Klugh ('23) points out that "the majority of plant ecologists agree that either the habitat or the vegetation itself, or both, furnish the basis of ecological classification and as in zooecology the vegetation is part of the habitat, the habitat is the only logical basis of a *common scheme* of classification."

*On a basis of flora or fauna.*—The plant association is emphasized by Nichols ('23) who has supported the position "that the term Plant Association be recognized as applicable both to the abstract vegetation concept and the concrete individual pieces of vegetation on which the concept is based." Tansley ('20) states that "it is most important to fix our attention on the plant community itself and to name it by its *dominant species,*" and Clements' ('28) terms, "consocies" and "consociation" have reference to an association *dominated by a single species.* On the other hand, many ecological classes, especially the large classes, are named from groups of plants or, *communities,* as forests and grasslands, containing many species.

*On a basis of succession or development.*—Clements ('28) states that: "As an organism the formation arises, grows, matures and dies," and Cowles has emphasized that classification should be both genetic and dynamic. The *climax* association is regarded as the ultimate basis of ecological classification by Weaver and Clements ('29); and by Shelford ('32) for animals, since animal communities may be grouped essentially with primary reference to their plant food. Placing plants in a primary position ecologically is another method of unifying the systems of the phyto-ecologist and of the zoo-ecologist.

*Classification complexes.*—Many have combined various classification systems to satisfy the manifold characteristics of a biotic association; the *complex associa-*

*tions* have been given *complex names* as northwestern mesophytic evergreen forest (Livingston and Shreve, '23), which includes geographic, habitat, life-form and climax association features.

The result is that today there exist as quasi-synonyms for a particular association the following: the northern pine belt (Sargent, 1884) and (Schimper, '03); northern hardwood forest (Frothingham, '15); the northeastern transition forest (Nichols, '23); the great lakes or Canadian forest (Hardy, '20); the St. Lawrence, Great Lakes Region (Harshberger, '11); the lake forest region (Weaver and Clements, '29) and the hemlock-white pine northern hardwood forest (Nichols, '35); all of which are comparable to the Canadian zone of Merriam (1898).

### 3. *A Possible Solution of the Ecological Classification Problem*

Each of the systems of classification mentioned above has its advantages and has made contributions to the study of life in relation to environment. The solution may lie not in supplanting any system but in a co-ordination by reference to a *standard* which is *numerically definite* and which is sufficiently *comprehensive* to act as a *common denominator*. The concept of *Bio-climatic Zones* represented by polygons, as described below is offered in partial fulfilment of this requirement.

### 4. *Bio-climatic Zones Represented by* • *Polygons*

*A standard scale of bio-climatic zones.* —A proposed standard scale for bio-climatic zones is presented in the form of a group of *ipse-radial polygons*. It is not proposed that this habitat scale should disturb the well established concepts of biotic associations; rather it is proposed that *this bio-climatic standard should be used to parallel and to equate other systems of ecological classification.*

In constructing the standard scale (fig. 4.A.) the minimal values for each climatic

factor are joined to form an inner symmetrical polygon; the maximal values are similarly joined to form an outer symmetrical polygon. The intervening area is divided equally by polygons to form three symmetrical and equi-radial zones. These are designated respectively as:

(1) *The Hypo-bio-climatic standard zone* (H)

(2) *The Meso-bio-climatic standard zone* (M)

(3) *The Super-bio-climatic standard zone* (S).

It may be noted that the standards of measurement used in science generally are "ideal" concepts and the "actual" matter or energy measured does not conform necessarily in its proportions; nor is it necessary that the entity should have a simple numerical relation to the standard. Similarly, the proposed standard zones are *bases of comparison* only and frequently are merely approached by bioclimatic phenomena.

The southeastern evergreen forest median falls marginally within the *super-bioclimatic zone,* except for the factor, hours of sunlight, which nearly approaches (fig. 4.B.).

The medians of the deciduous forest and of the grassland deciduous forest transition form closely parallel polygons which lie within the *meso-bio-climatic zone,* except for an extension into the super-bio-climatic zone in the region of humidity and evaporation (fig. 4.B.).

The northeastern mesophytic evergreen forest median is *asymmetrically located in each of the three bio-climatic zones;* the super-zone with respect to humidity and evaporation, the meso-zone with respect to mean precipitation, and the hypo-zone with respect to the light, temperature and physiological summation factors (fig. 4.C.).

The hygrophytic forest median is very similar to that of the northeastern mesophytic forest except that the days of the frostless season characteristic is in the meso-zone (fig. 4.C.).
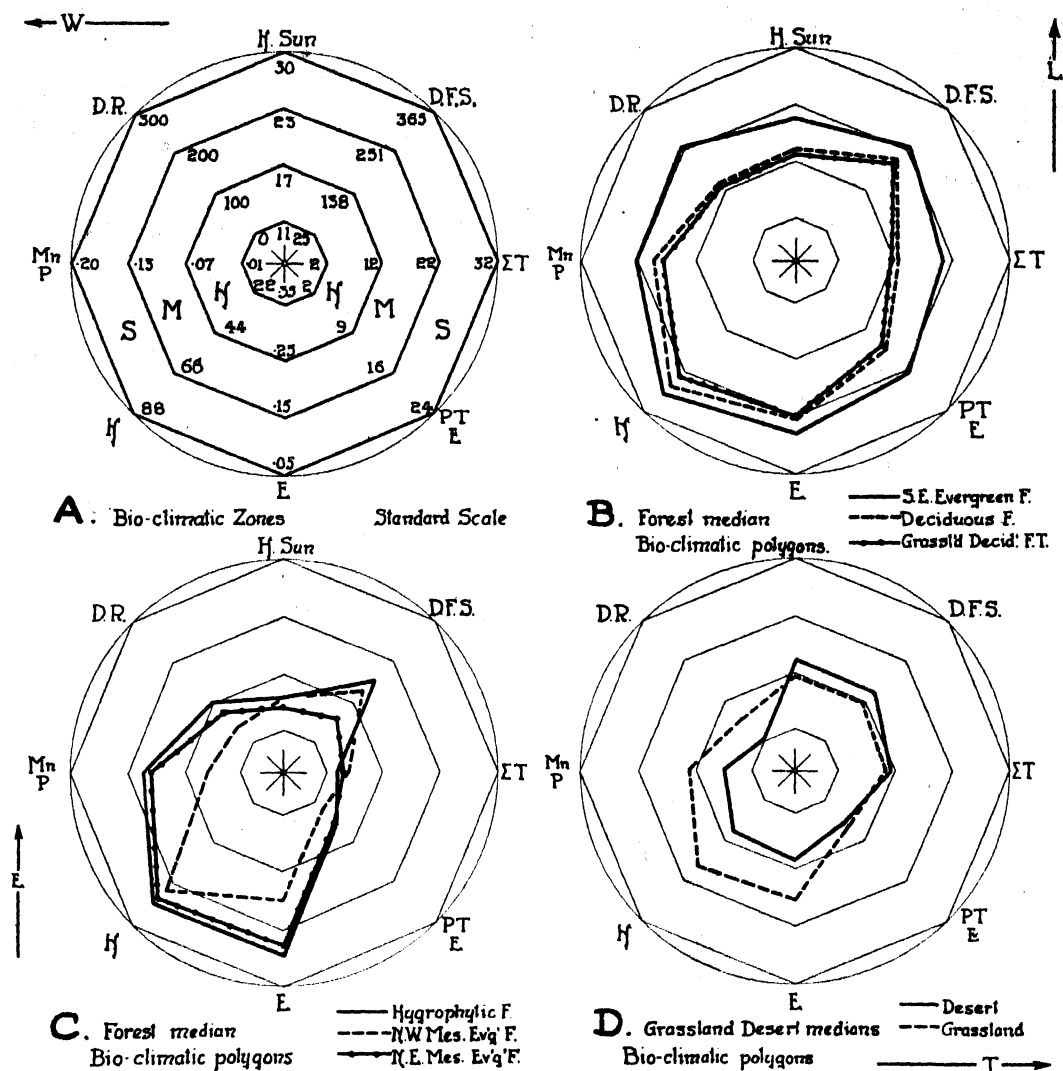
FIG. 4. **A.** Bio-climatic Zones, Standard Scale. The ranges between the various climatic extremes for the factors indicated are represented as radii which are trisected and the corresponding points connected to form three standard bio-climatic zones: the hypo-bioclimatic zone (H) ; the meso-bioclimatic zone (M) and the super-bioclimatic zone (S).

**B.** The bio-climatic median polygons for the Southeastern Evergreen Forest, the Deciduous Forest and the Grassland Deciduous Forest Transition are evaluated by superposition with reference to the bio-climatic standard scale.

**C.** Similarly, the bio-climatic medians for the Hygrophytic Forest, the Northwestern Mesophytic Evergreen Forest and the Northwestern Mesophytic Evergreen Forest are evaluated by reference to the bio-climatic standard scale.

**D.** Similarly, the bio-climatic medians for the Desert and Grasslands are evaluated with reference to the bio-climatic standard scale.

The northwestern mesophytic evergreen forest median is *hypo-bio-climatic* except for meso-zone extensions for evaporation and days of the frostless season factors and a super-zone extension for the humidity factor (fig. 4.C.).

The grassland median is *hypo-bio-climatic* except for meso-zone extensions in the regions of the mean daily precipitation, the humidity and the evaporation factors (fig. 4.D.).

The desert is *hypo-bio-climatic* except

for extensions in the regions of the *light* and *frostless days factors*, which are meso-zonal (fig. 4.D.).

It is believed that *by equating the vegetation areas of the United States to bioclimatic zone standards*, having definite numerical values, and as *represented by polygonal graphs, a greater co-ordination has been effected.* It is suggested that by the use of similar bio-edaphic and biotic

standards a further organization of ecological phenomena may accrue.

## THE COMMON RANGE AND DIFFERENTIATING LIMITS OF SPECIFIC FORMS AS REPRESENTED BY POLYGONAL GRAPHS (fig. 5)

A comparison of the bio-climatic ranges of specific forms, as represented by polygonal graphs gives a definite determina-
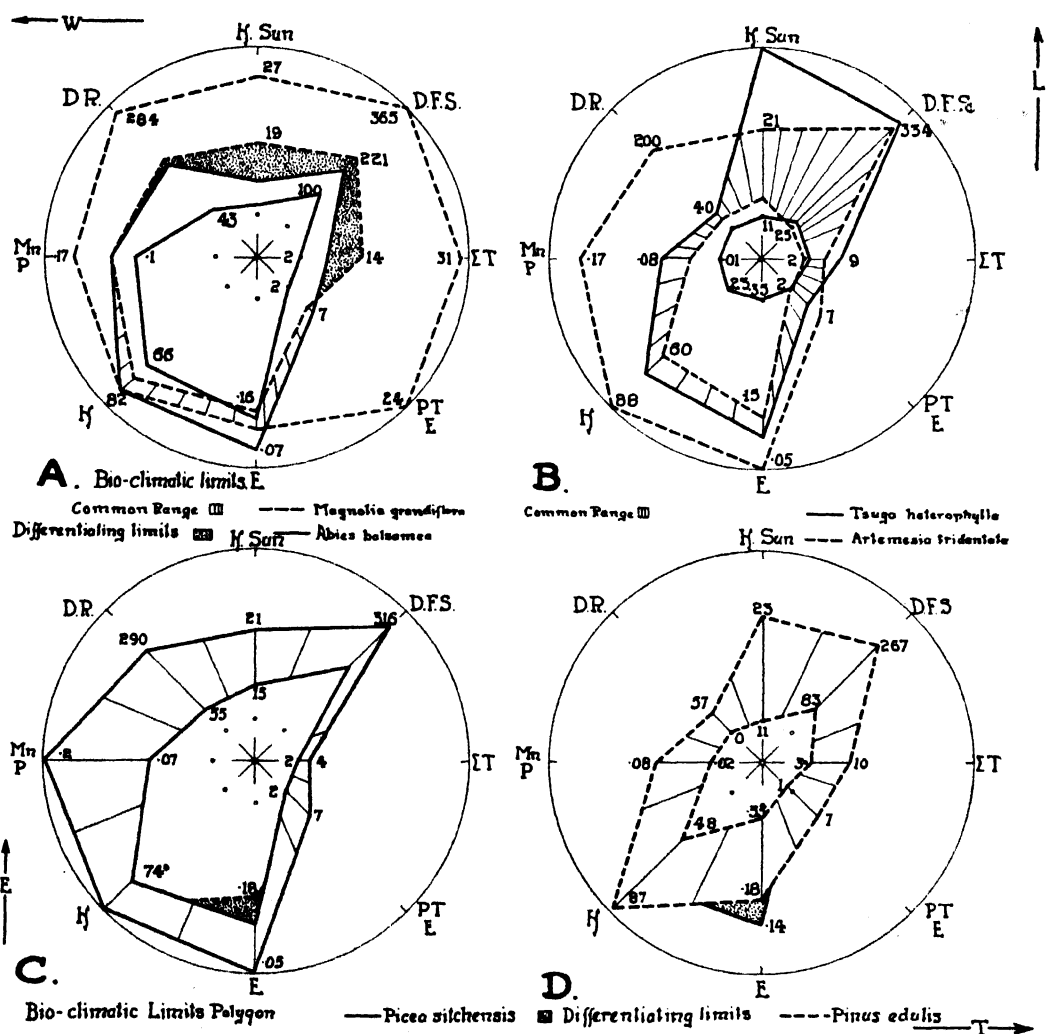


FIG. 5. **A.** By superimposing the polygons representing the bio-climatic limits of *Magnolia grandiflora* and *Abies balsamea* the common range and the differentiation limits, with reference to the factors indicated, are denoted.

**B.** Similarly, by superimposing the polygons representing the bio-climatic limits of *Tsuga heterophylla* and *Artemisia tridentata* the limited common ranges are indicated for each of the factors considered and the cumulative effect noted.

**C, D.** The adjacent figures representing the bio-climatic extremes of *Picea sitchensis* and *Pinus edulis* indicate that the differentiating factor is humidity; for other factors there is a limited common range, bio-climatically.

tion of the common climatic range and the differentiating climatic limits of these forms.

The minimal and maximal climatic polygons are superimposed for the large flowered magnolia (*Magnolia grandiflora*) and for the balsam fir (*Abies balsamea*) in figure 5.A. There is a narrow common range for these forms in the region of humidity, evaporation and the physiological values regions of their ranges; while their limits are differentiating and consequently their *ranges are mutually exclusive with respect to the light, temperature, days of the frostless season and days of rain.*

Similarly figure 5.B. represents superimposed bio-climatic polygons for the western hemlock (*Tsuga heterophylla*) and the small sage-bush (*Artemisia tridentata*). The ranges of tolerance of these species have *a common zone* for all the factors represented in the graph and it is evident that, on this basis, the two species are not mutually exclusive. The common range toward many of the factors, days of the rainy season, mean daily precipitation, humidity, evaporation, temperature, and physiological values are all narrow, each factor reducing the probability of their coincident occurrence; *the cumulative effect is one of practical mutual exclusion.* The polygons for the bio-climatic limits of the sitka spruce (*Picea sitchensis*) and of the nut pine (*Pinus edulis*) are placed adjacent, for purposes of comparison, and the zone between the differentiating limits is stippled in each case (fig. 5.C, D.).

In addition to the use of the sitka spruce and the nut pine as characteristic dominants or sub-dominants of the hygrophytic forest and the northwestern mesophytic evergreen forest respectively, the polygons demonstrate that the *evaporation factor is that which is primarily responsible for the differentiating limits* of these trees of the western United States.

The polygonal graphs of specific forms give evidence that *any factor* or *group of factors may act as a differentiating opera-*tive in determining the occurrence of specific species or groups of species.

## SUMMARY

1. The environment of plants and animals is a complex, composed of various, more or less inter-related factors, climatic, edaphic and biotic.

2. The problem of solving the effect of the complex environment on the growth and the distribution of living forms has been attacked from many points; by the control of conditions; by the study of a single variable; by the elimination of favorable factors to observe a single determining factor; by statistically correlating parallel or coincident effects of separate factors or groups of factors; by using the biologic units of measurement, "indicators" or "dominants."

3. Polygonal graphing, which presents a composite concept of several factors in the form of polygon contours, is offered as a method of recording complex natural conditions.

4. Polygons, correlating eight climatic factors, data as recorded by Livingston and Shreve, for the vegetation areas of the United States, are presented.

5. Ipse-radial polygons, representing the minimal, maximal and medial values for these eight climatic factors of each vegetation area, are used to compare the ecological complexes.

6. The desirability of co-ordination between the various systems of ecological classification is recognized.

7. Polygons of standard bio-climatic zones are presented as basic units or reference standards, with numerical limits, for the equating of ecological classes.

8. Three standard bio-climatic zones are proposed: hypo-bio-climatic; meso-bio-climatic and super-bio-climatic.

9. The medial bio-climatic polygons of vegetation areas are equated to the bio-climatic standards.

10. The bio-climatic common range and the differentiating factors of distribution, for several species, are determined

by reference to the polygons representing bio-climatic minimal and maximal values.

## CONCLUSION

It is suggested that the consideration of polygonal graphing as a method of establishing bio-climatic, bio-edaphic, and biotic standards would facilitate the progress of ecology.

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# THE LOCOMOTOR ACTIVITY OF THE GOLDFISH, CARASSIUS AURATUS L., UNDER VARIOUS CONDITIONS OF HOMOTYPIC AND HETEROTYPIC GROUPING

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The investigations reported here represent a continuation of research on one of the aspects of the mass physiology of animals—the effect of grouping on the locomotor activity of fishes (Shlaifer, '38, '39). Schuett ('34) found that an isolated goldfish, Carassius auratus L., was more active in an aquarium than were fishes in a group of four in the same volume of water. Escobar, Minahan, and Shaw ('36) and Breder and Nigrelli ('38) confirmed these findings. Shlaifer ('38) measured the activity of C. auratus indirectly through oxygen consumption and directly by an observational technique described below. He found, among other things, that an isolated animal consumed more oxygen and had a higher rate of locomotor activity than did an individual in a group of two or of four. In an analysis of this well-established "group effect," Shlaifer ('39) demonstrated that vision is the primary sensory modality in the phenomenon. The group effect is lost when fishes are placed in the dark or are blinded. On the other hand, the activity of isolated animals is decreased when they are placed in contact through vision alone with others of the same species, with their own mirror images, or with recently killed and mounted specimens. It was also shown that the inhibition of activity in the grouped animals is probably due to the perception of the form rather than the color or movement of the individuals comprising the group.

The work reported below represents an attempt to determine the effect of heterotypic grouping on the locomotor activity of C. auratus. Such experiments, among other things, may be utilized to determine whether the reaction of a goldfish to the body form of others in the group is a response to the particular type of body form characteristic of the species or to body form of fishes in general.

## MATERIALS AND METHODS

With the exception of A in tables 1 and 2, the data for which were obtained at the Whitman Laboratory for Experimental Zoology of the University of Chicago, the experiments reported here were performed in the laboratory of the New York Aquarium. The writer wishes to express his appreciation to Dr. C. M. Breder, Jr., for the use of laboratory facilities and to Mr. R. S. Mathews for assistance during the course of the work.

All experiments were performed between the hours of 10:00 A.M. and 1:00 P.M. The temperature range was 20°–22° C. At Whitman Laboratory tap water, filtered free of chlorine and sediment, was used; at the Aquarium the water, originally drawn from the tap, was taken from a large stock tank that contained several species of small tropical fresh-water fishes and may therefore be termed "conditioned." The dimensions of the 7.5-liter aquaria used at Whitman were 25 cm. by 30 cm. and 13 cm. deep at the six liter mark. At the Aquarium the 15-liter aquaria employed were 30 cm. by 21 cm. and 17 cm. deep at the twelve liter mark. The experimental animals, Carassius auratus L., were young specimens of the "common comet" variety, 4–5 cm. in length and more or less streamlined. (See fig. 6.) The body color of the animals was uniformly orange or gold but the variable orange, gold, and white color patterns in the tail facilitated the use of individual records of activity. The fishes at Whitman were fed oats twice a week while those at the Aquarium re-

ceived *Tubifex* three times a week. The animals were always fed at the conclusion of a day's experiments and were not used for at least 21 hours thereafter.

The technique employed in measuring locomotor activity was that first described by Escobar and associates ('36) except that all observations were made by one person. Aquaria of the dimensions and capacities listed above were marked off with red India ink into 5-cm. squares on all four sides. Since not all of the dimensions of the aquaria were multiples of five, some of the boxes were rectangles rather than squares. However, movement of a fish into one of these smaller boxes was considered equivalent to movement into the larger squares, since the variable was the same for the various types of grouping. The 5-cm. squares, when viewed in space, constitute a series of imaginary cubes of 125 cc. capacity through which the animals pass when swimming. The eye of the fish was used as the anatomical landmark in judging whether it had passed from one cube into another. The swimming of the individual from one cube into another constitutes a "movement." More complete discussion of the technique may be found elsewhere (Shlaifer, '38).

The measurement of the amount of oxygen consumed is undoubtedly a more sensitive technique in determining activity than is the observational method described above even though the former is indirect and the latter direct (Shlaifer, '39). However, this method obviously cannot be used when heterotypic groups are being studied. The "ichthyometer" described by Spencer ('39) is not well adapted for the measurement of the activity of an animal in a group. Thus, the observational technique described above was the only method which could be used in a standardized way for all experiments. The sources of error are negligible when a sufficient number of tests are performed.

All experiments were carried through a three-hour period each day. The test animals were alternated daily between the control and experimental states at the conclusion of a day's experiments; thus, a 21-hour period of acclimation obtained.

EFFECT OF HETEROTYPIC GROUPING

Escobar, Minahan, and Shaw ('36) measured the activity of *C. auratus* in a heterotypic group of four fishes; the other species used were *Gambusia affinis*, *Oryzias latipes*, and *Macropodus verdiauratus*. It was found that in such a heterotypic group the activity of the goldfish was not only greater than it was in a homotypic group of four but even exceeded somewhat the activity of an isolated goldfish. A statistical analysis, however, was not given. The above investigators state further: "In the case of animals with highly developed visual sense organs, the contour and coloration of their fellows in homotypic and heterotypic groups may conceivably alter their movements resulting in various degrees of aggregation or dispersal."

Breder and Nigrelli ('38) state that the evidence from the mating behavior of fishes in which the animals may attempt to mate with unfish-like objects does not support this view. On the other hand, Noble and Curtis ('39) demonstrate that *Hemichromis bimaculatus* is apparently capable of making rather fine distinctions in the contour and coloration of fishes as well as in their behavior.

Reighard ('13) indicates that heterotypic fish schools are not uncommon and those of young animals are often of an ecological nature rather than a specific one.

The experiments described below were designed to extend the work of Escobar, Minahan, and Shaw ('36) on the effect of heterotypic grouping on the locomotor activity of the goldfish. The species used were selected for considerable variation in form, the major factor involved in the visual response of *C. auratus* to others of its kind (Shlaifer, '39). However, the swimming movement of these species, while in all cases carangiform,

also differed appreciably from that of the goldfish.

*Materials and Methods.*—The locomotor activity of *C. auratus* was measured daily in homotypic and heterotypic groups. The homotypic group in all cases consisted of four goldfishes. Records were obtained on eight specimens of equal size. Test fishes were alternated each day between the control homotypic group and the experimental heterotypic group of four individuals. Specimens that were used as test animals for a period of days were subsequently used as non-test fishes in the homotypic group. Activity records were taken of all animals in homotypic and heterotypic grouping so that the factor of total amount of move-

TABLE 1. *Effect of heterotypic grouping on the locomotor activity of the goldfish*

| Experimental condition | Homotypic group [1] | | Heterotypic group | | Mean difference | P-value [*] |
|---|---|---|---|---|---|---|
| | No. of cases [2] | Mean activity [3] | No. of cases [2] | Mean activity [3] | | |
| A [4, 6] | 30 | 133.0 | 30 | 187.6 | 54.6 | 0.0044 |
| B [5, 7] | 16 | 146.8 | 16 | 254.3 | 107.5 | 0.0002 |
| C [5, 8] | 16 | 198.4 | 16 | 386.6 | 188.2 | 0.0000 |
| D [5, 9] | 16 | 137.3 | 16 | 159.4 | 22.1 | 0.1251 |

[*] Upper limit of statistical significance is set at 0.05. This is three times the probable error. $P = 0.01$ indicates good significance, while a value of 0.100 or more indicates little significance ("Student," 1925).
[1] Contains test goldfish and three other goldfishes.
[2] Each case is the average of three 10-minute observation periods.
[3] The activity of the test goldfish expressed in "movements" per 10-minute period of observation. See "Materials and Methods" for explanation of the term "movement."
[4] Volume is six liters of water in a 7.5-liter aquarium.
[5] Volume is twelve liters of water in a 15-liter aquarium.
[6] Heterotypic group contains test goldfish and three *Notropis rubrifrons.*
[7] Heterotypic group contains test goldfish and three *Aequidens portalegrensis.*
[8] Heterotypic group contains test goldfish, one *A. portalegrensis*, one *Xiphophorus hellerii*, and one *Barbus partipentazona*(?).
[9] Heterotypic group contains test goldfish, one other goldfish, and two *A. portalegrensis.*

TABLE 2. *Comparing the activity of the non-test fishes in the homotypic group with that of the non-test fishes in the heterotypic group*

| Experimental condition | Homotypic group [1] | | Heterotypic group | | Mean difference | P |
|---|---|---|---|---|---|---|
| | No. of cases [2] | Mean activity [3] | No. of cases [2] | Mean activity [3] | | |
| A [4, 6] | 30 | 67.5 | 30 | 46.8 | 20.7 | 0.0094 |
| B [5, 7] | 16 | 70.0 | 16 | 62.4 | 7.6 | 0.3519 |
| C [5, 8] | 16 | 98.0 | 16 | 118.7 | 20.7 | 0.0128 |
| D [5, 9] | 16 | 63.7 | 16 | 54.6 | 9.1 | 0.1869 |

[1] Consists of three non-test goldfishes.
[2] Each case is the average of nine 5-minute observation periods.
[3] The average activity of the three non-test fishes expressed in "movements" per fish per 5-minute period of observation.
[4] Volume is six liters of water in a 7.5-liter aquarium.
[5] Volume is twelve liters of water in a 15-liter aquarium.
[6] Non-test fishes in the heterotypic group are three *Notropis rubrifrons.*
[7] Non-test fishes in the heterotypic group are three *Aequidens portalegrensis.*
[8] Non-test fishes in the heterotypic group are one *A. portalegrensis*, one *Xiphophorus hellerii*, and one *Barbus partipentazona*(?).
[9] Non-test fishes in the heterotypic group are one goldfish and two *A. portalegrensis.*

ment was not an unknown variable. In *A* of tables 1 and 2, the species used for the heterotypic condition was *Notropis rubrifrons* Cope. The specimens selected were young forms, 5–6 cm. in length, olive-green in color, narrow-bodied, and sharply streamlined. (See fig. 2.) The goldfishes used in this set were of a different lot from others since this experiment was performed at Chicago. In *B*, 4–5 cm. specimens of *Aequidens portalegrensis* Hensel were used. These cichlids were young, also olive-green in color, but stout-bodied in form. (See fig. 1.) In *C*, the heterotypic group was composed of three different species in addition to *C. auratus*. One of the species was *A. portalegrensis*, described above. The other two were *Xiphophorus hellerii* Heckel and *Barbus*, probably *Barbus partipentazona* Fowler. The specimens of *X. hellerii*, the sword-
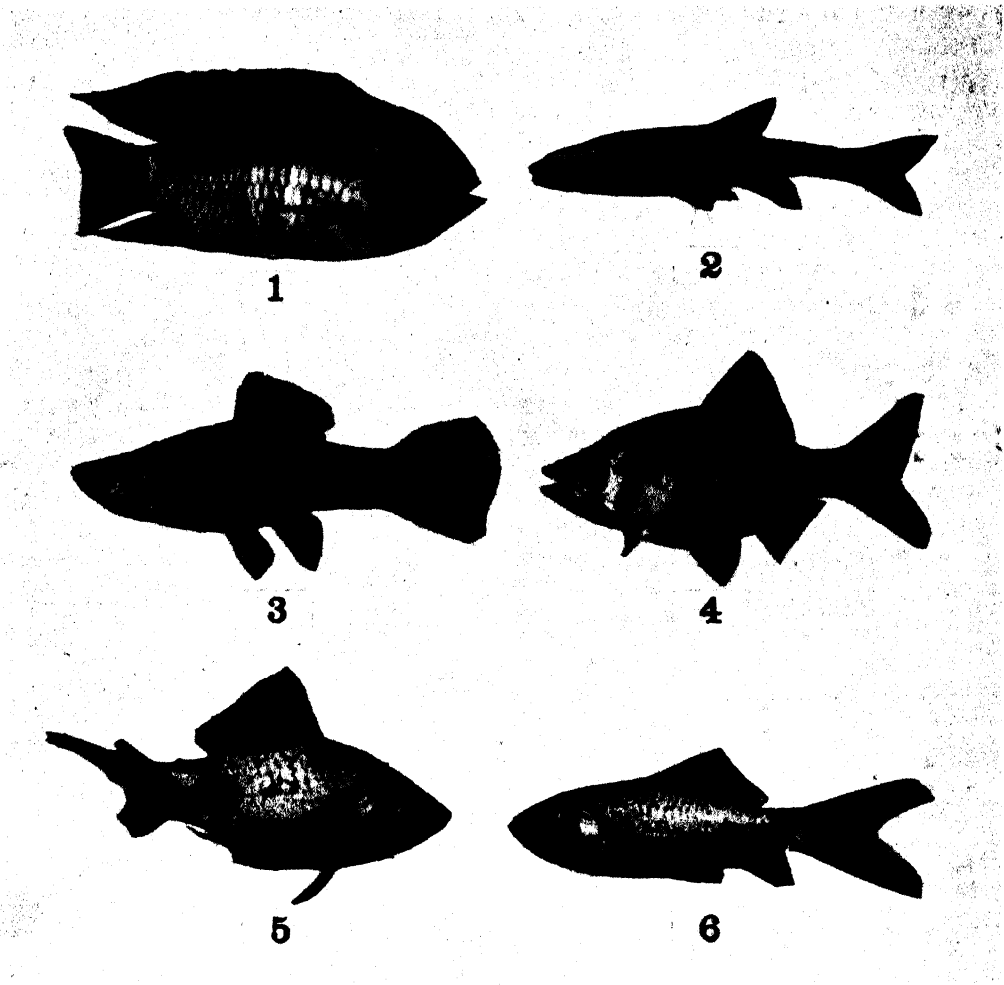
EXPLANATION OF FIGS. 1–6

FIG. 1. *Aequidens portalegrensis.*
FIG. 2. A Cyprinid minnow illustrating the body form of *Notropis rubrifrons.*
FIG. 3. *Xiphophorus hellerii.*　　FIG. 5. *Carassius auratus*—"fan-tail" variety.
FIG. 4. *Barbus partipentazona* (?).　FIG. 6. *Carassius auratus*—"common comet" variety.

tail, were sexually mature females, 6 cm. in length, again olive-green in color, and moderately full-bodied. (See fig. 3.) The barbs were mature specimens, 3–4 cm. in length, with yellow bodies traversed by four vertical black stripes and whose form, rounded in contour and thin in cross-section, somewhat resembled that of a stoutish goldfish. (See fig. 4.) With the exception of the sword-tails, sex was not determined. In *D*, the experimental condition might be termed "modified" heterotypic grouping. It was com-

posed of the test goldfish, two *A. portalegrensis,* and one other goldfish.

Each test animal was observed for ten minutes and each non-test animal for five minutes during each of the three experimental hours.

*Results.*—Reference to table 1 shows that the effect of grouping on the locomotor activity of the goldfish is completely lost when the heterotypic group is composed entirely of specimens of other species. In *A, B,* and *C,* there is high statistical significance. On the other

hand, when there is only one other gold-fish in the otherwise heterotypic group (condition $D$), the group effect is maintained. In view of the fact that *C. auratus* is not a strongly schooling species this result is interesting. It is, however, to be expected in view of previous results obtained by the writer ('38). It was found that the locomotor activity and oxygen consumption of each goldfish in a group of two tended to be the same as that of each animal in a group of four.

Reference to table 2 indicates that in *A, B,* and *D,* the total activity of the non-test animals is not higher in the heterotypic group. In fact, in *A* the homotypic group is significantly more active than is the heterotypic group of non-test animals. Thus, the greater activity of *C. auratus* in the heterotypic groups cannot be attributed to the greater movement of the specimens comprising those groups. In *C* of table 2, the heterotypic group is significantly more active than is the homotypic group, due mainly to the rather rapid-moving barbs. However, the difference between the means in *C* of table 2 is relatively small in comparison with the difference between the means in *C* of table 1. The same applies to the degree of statistical significance. Thus, it is indicated that here, too, total activity in the heterotypic group is not the causal factor. In this case, however, there is a slight complicating factor in the proclivity of the barb to chase the goldfish at times, so that we do not have a complete condition of "tolerance" in so far as that state can be detected through observation. In no other experiment reported here was there chasing of the test goldfish by other individuals.

The activity of the non-test goldfish of the homotypic group as listed in table 2 is recorded in five-minute periods of observation. These same animals were used as test specimens in table 1 where the activity is recorded in ten-minute periods. If the mean activities under "Homotypic Group" in these tables are compared, it is seen in each case that when the activity

in table 2 is multiplied by two it is remarkably close to that of table 1. Thus, it is demonstrated that the technique used for measuring locomotor activity gives consistent results over a long period of time.

It may be concluded that the failure to obtain a group effect in *C. auratus* when it is placed with other species is not due to the greater activity of those species. The results obtained by the writer ('39) also indicate that response to color difference is not involved. Hence, there remain the factors of form and type of movement. Some of the experiments described below attempt to isolate these factors.

## EFFECT OF SUNFISH MODELS

Breder and Nigrelli ('35) state that a schooling fish primarily holds a position of maximum "comfort" by fixing its vision on some object, either a stationary one or a moving one; this difference determines whether the fish maintains a stationary position or moves forward. Working with the goldfish they further state ('38): "Since the aggregating tendency implies an urge to seek a position close to but not in contact with some object (another fish), it may also be that approach to some inanimate object or surface is used as a substitute to partially satisfy that urge when no companions are present." When this inanimate object is a killed and mounted goldfish (Shlaifer, '39), the "aggregating urge" is apparently satisfied. In fact, visual contact with these mounted forms reduces the activity of isolated goldfishes even more than does visual contact with normal free-swimming individuals. Thus, visual response to form is the causal factor in the effect of grouping on *C. auratus* when it is placed with others of its kind.

Spooner ('31) found that the bass, *Morone labrax,* would be attracted to a dead mounted fish supported by glass in the position of a live resting animal; however, several rough kinds of models failed to attract the fish. Breder and Coates

('35) investigating the sex recognition of the guppy, *Lebistes reticulatus,* find that no reaction is given to carefully made models of female *Lebistes* either inside or outside the aquarium and with or without movement. On the other hand, Lissmann ('32) finds that the characteristic fighting reaction of the Siamese fighting fish, *Betta splendens,* is elicited by plasticine models or paintings of the fish.

It is desirable to know whether any inanimate fish-like object will be reacted to by the goldfish in terms of differential locomotor activity. The experiments described below attempt to attack this problem.

*Materials and Methods.*—In *A* of table 3, goldfishes were alternated daily between the control condition of complete isolation and the experimental condition. In the latter state three sunfish models were suspended by very fine wire into the 15-liter aquarium. They were placed in a normal horizontal swimming position three centimeters above the floor of the

TABLE 3.    *Effect of sunfish models on the locomotor activity of isolated goldfishes*

| Conditions of the experiment | Control | | Experimental | | Mean differ-ence | P |
|---|---|---|---|---|---|---|
| | No. of cases | Mean activ-ity [b] | No. of cases | Mean activ-ity [b] | | |
| A [1, a] | 16 | 260.3 | 16 | 246.3 | 14.0 | 0.5381 |
| B [a, c] | 16 | 222.4 | 16 | 222.6 | 0.2 | None calculated |

[1] In the control condition, the experimental animal is isolated in twelve liters of water in a 15-liter aquarium. In the experimental state, there are three sunfish models suspended in the aquarium.

[a] In the control condition, the experimental animal is isolated in twelve liters of water in a 15-liter aquarium which is placed inside a 50-liter aquarium. In the experimental state, the isolated goldfish is in visual contact with three sunfish models that are suspended in the large aquarium next to the long sides of the small aquarium.

[a] Each case is the average of three 10-minute observation periods.

[c] Each case is the average of six 10-minute observation periods.

[b] The activity of the isolated goldfish expressed in "movements" per 10-minute period of observation.

aquarium, the level at which isolated *C. auratus* usually swim. Two models were placed next to one long side of the aquarium pointed in the same direction about 7.5 cm. apart. The third model was placed next to the opposite long side of the aquarium at a position roughly in between that of the other two models. These models were composed of solder-like metal, 5 cm. in length, colored green and black dorsally and yellow ventrally, and having the stout-bodied form of a generalized small sunfish. To prevent the leaching out of metallic ions into the medium, the models were coated with lacquer.

In *B* of table 3, the animal in the control condition was again placed in isolation; the 15-liter aquarium, however, was centrally placed inside a 50-liter aquarium whose dimensions were 56 cm. by 30 cm. and 28 cm. deep. This large aquarium was filled with about fourteen liters of water up to the 12-liter mark on the smaller aquarium. In the experimental state the models were suspended in the same way as in *A* but inside the large aquarium next to the outer surface of the smaller one.

Thus, in *A* the experimental animal may be in actual contact with the models while in *B* there is only visual contact. There was an interval of several weeks between tests *A* and *B*. In *A* the test goldfish was observed during one ten-minute period and in *B* during two ten-minute periods in each of the three experimental hours.

*Results.*—Reference to table 3 indicates that there is no significant difference in activity between the control and the experimental states. The means are almost identical. In *A* the goldfish would often collide accidentally with the models but exhibited no fright reaction. Such contacts are relatively rare in a group of free-swimming *C. auratus.*

It may be concluded, then, that the presence of any inanimate fish-like object is not sufficient to induce the group effect. Also, inasmuch as a killed and mounted

goldfish (Shlaifer, '39) does induce this effect, it is apparently a difference in contour which is the major factor.

## VISUAL CONTACT WITH THE SAME AND OTHER SPECIES

The experiments described below were designed to analyze further the effect of heterotypic grouping, with all factors but vision eliminated. Shlaifer ('39) found that visual contact by an isolated goldfish with three others of its kind was effective in producing a group effect. In fact, this visual response to other *C. auratus*, taken alone, induced a reduction in activity of the same order of magnitude as is obtained when an individual is an actual member of a group of four. Welty ('34) in the course of his experiments on learning in the goldfish showed that these animals learn to swim a maze more rapidly after having seen, through transparent glass, others of their kind perform in it.

*Methods.*—In all of the experiments listed in table 4, the aquarium set-up was similar to that described for *B* of table 3. The difference in dimensions between the large and small aquaria was easily sufficient to permit free swimming by any forms placed in the large one. In all cases the test goldfish in the control condition was in complete isolation in the small aquarium in twelve liters of water.

*A* of table 4 is a repetition of the experiment described above (Shlaifer, '39) except that the technique used for the measurement of locomotor activity was observational rather than the chemical method of determining oxygen consumption. In the experimental state there were three normal swimming goldfishes in the large aquarium.

In the experimental condition of *B*, three normal swimming *Barbus partipentazona* (?) were placed in the outer aquarium. It will be recalled that when this barb was one of the three different species with which *C. auratus* was placed in the heterotypic group of four (*C* of tables 1 and 2), there was no group effect. Also, a complicating factor present in

that experiment was the occasional chasing of the goldfish by the barb. The experimental set-up used here eliminated that possibility.

In the experimental state in *C* of table 4, three *Aequidens portalegrensis* were killed and injected with formaldehyde and placed in the larger aquarium in a manner similar to that described for the models in *B* of table 3, except that they were supported from below on looped wire bases instead of being suspended from above. In this experiment as in the sunfish model tests, the experimental animal can be responding to form only. (See Shlaifer, '39, for the treatment of the color question.) It should also be noted that these injected cichlids were relatively more lifelike than sunfish models.

The test goldfish in all cases in table 4 was observed each hour of the three-hour experimental period for two ten-minute periods.

TABLE 4. *Effect of visual contact with the same and other species on the locomotor activity of isolated goldfishes*

| Conditions of the experiment | Control [1] | | Experimental | | Mean difference | P |
|---|---|---|---|---|---|---|
| | No. of cases [2] | Mean activity [3] | No. of cases [2] | Mean activity [3] | | |
| *A* [4] | 16 | 349.3 | 16 | 252.4 | 96.9 | 0.0187 |
| *B* [5] | 16 | 485.6 | 16 | 394.1 | 91.5 | 0.0771 |
| *C* [6] | 16 | 257.8 | 16 | 270.0 | 12.2 | 0.5381 |

[1] A goldfish in isolation in twelve liters of water in a 15-liter aquarium placed inside a 50-liter aquarium.

[2] Each case is the average of six 10-minute observation periods.

[3] The activity of the isolated goldfish expressed in "movements" per 10-minute period of observation.

[4] In the experimental state the isolated goldfish is in visual contact with three normal goldfishes placed in the large aquarium.

[5] In the experimental state the isolated goldfish is in visual contact with three normal *Barbus partipentazona*(?) placed inside the large aquarium.

[6] In the experimental state the isolated goldfish is in visual contact with three killed and mounted *Aequidens portalegrensis* placed in the large aquarium next to the long sides of the small aquarium.

*Results.*—*A* of table 4 confirms the previous results for this experiment in which the oxygen consumption was measured. It is seen that visual contact with others of the same species will induce a group effect.

The data in *C* are similar to those obtained with sunfish models. Again it is seen that visual contact with any fish, regardless of form, will not reduce the activity of *C. auratus.* It may also be recalled here that when the goldfish is placed with three free-swimming *A. portalegrensis* (*B* of table 1) there is also no group effect.

It is seen in *B* that visual contact with free-swimming barbs does not produce a significant decrease in activity. However, the *P*-value is close to that commonly accepted as significant (0.05). This may well be correlated with the fact that these barbs, in general, resemble the goldfish more than the other species used.

It will be noted that the mean activities in the control condition of complete isolation in *A, B* and *C* are appreciably different. Since these experiments were carried out more or less simultaneously, different individuals were used for each condition. Individual variations in activity are easily great enough to account for these differences.

## GROUPING WITH A DIFFERENT VARIETY OF THE SAME SPECIES

The results obtained seem to indicate that, as far as tested, the group effect in the goldfish, is species specific. However, the evidence does not point to any mysterious species attraction but rather to a more or less mechanical visual response to form. If so, it was thought that grouping with a variety of goldfish differing in form from the one used thus far might help to confirm this hypothesis.

*Methods.*—The variety of *C. auratus* previously used in these experiments is the "common comet" type whose description has already been given. In the control condition in table 5 the test "common comet" was grouped with three others of

the same variety. In the experimental state, the common comet was grouped with three "fan-tails." These were of the same length and color as the common comets. However, they differed in form, being rather stout-bodied and possessing a "double" tail spread somewhat in the manner indicated by their name. (See fig. 5.) Their swimming movement was also more jerky and less uniform than that of the common comet.

The activity of the test goldfish was observed for ten minutes of each of the three experimental hours; the non-test individuals were observed for five minutes of each experimental hour.

TABLE 5.  *Effect of grouping with a fan-tail variety on the locomotor activity of a common comet variety of goldfish*

| Control [1] | | Experimental [2] | | Mean differ-ence | P |
|---|---|---|---|---|---|
| No. of cases [3] | Mean activity [4] | No. of cases [3] | Mean activity [4] | | |
| 16 | 181.9 | 16 | 204.0 | 22.1 | 0.0474 |

[1] The activity of a common comet in a group containing three others of the same variety in twelve liters of water in a 15-liter aquarium.
[2] The activity of a common comet placed with a group of three fan-tails in the same volume.
[3] Each case is the average of three 10-minute periods of observation.
[4] Expressed in "movements" per fish per 10-minute period of observation.

*Results.*—The data in table 5 indicate that though the mean difference is rather small, it is statistically significant although close to the accepted upper limit. Reference to table 6 shows that total activity is not a factor, being the same in both control and experimental. Again, if the mean activity for the five-minute period of observation in the control state in table 6 is multiplied by two, it is equivalent to the activity in the control state in table 5 for a ten-minute period. Since the individuals used in both of these states were the same, the consistency of the measuring technique is again demonstrated.

Thus, if the test goldfish is placed with others of its species differing appreciably in form, the locomotor activity is signifi-

TABLE 6. *Comparing the activity of the three common comets used in the control condition with that of the three fan-tails used in the experimental condition*

| Control [1] | | Experimental [2] | | Mean differ-ence | P |
|---|---|---|---|---|---|
| No. of cases [3] | Mean activ-ity [4] | No. of cases [3] | Mean activ-ity [4] | | |
| 16 | 91.1 | 16 | 91.2 | 0.1 | None calculated |

[1] The average activity of the three common comets.
[2] The average activity of the three fan-tails.
[3] Each case is the average of nine 5-minute periods of observation.
[4] Expressed in "movements" per fish per 5-minute period of observation.

cantly increased. However, this should not be taken to mean that there is no group effect but rather that the effect is reduced in intensity.

## VISUAL CONTACT WITH MOUNTED FAN-TAILS

The experiment described above does not eliminate the factor of the type of movement since the fan-tails did swim in a manner slightly different from that of the common comets. Accordingly, the following experiment was utilized to isolate the factor of form.

*Methods.*—The aquarium set-up was similar to that previously described for visual contact experiments. In the control condition the isolated common comet in the small aquarium was in visual contact with three killed and mounted common comets set up in a manner described for *C* of table 4. In the experimental condition the test animal was in visual contact with three killed and mounted fan-tails arranged in the same manner as the common comets. While the formaldehyde injection did not affect the color of the fan-tails, it caused the mounted comets to lose their color and to become white in a few hours. However, once injected, the general appearance of the mounted animals was satisfactorily maintained so that it was not necessary to replace them during the course of the ex-

periments. The test animal was observed for ten minutes of each of the three experimental hours.

*Results.*—The data in table 7 indicate as they did in table 5 a small but significant increase in activity when the experimental common comet is in visual contact with mounted fan-tails. Form alone can be involved in this reaction. The accidental bleaching of the mounted common comets furnished an excellent control for response to color. Despite the

TABLE 7. *Effect of visual contact with killed and mounted fan-tails on the locomotor activity of isolated common comets*

| Control [1] | | Experimental [2] | | Mean differ-ence | P |
|---|---|---|---|---|---|
| No. of cases [3] | Mean activity [4] | No. of cases [3] | Mean activity [4] | | |
| 16 | 172.4 | 16 | 201.2 | 28.8 | 0.0428 |

[1] The activity of an isolated common comet in twelve liters of water in a 15-liter aquarium in visual contact with three killed and mounted common comets.
[2] The activity of an isolated common comet in the same volume of water in visual contact with three killed and mounted fan-tails.
[3] Each case is the average of three 10-minute periods of observation.
[4] Expressed in "movements" per 10-minute period of observation.

loss of the normal gold or orange color by the injected common comets, visual contact with these forms produced a significant reduction in the activity of the experimental animals over that manifest when these individuals were in visual contact with goldfishes of normal color but of different shape. A further treatment of the implications of the data in tables 5 and 7 will be found below.

## DISCUSSION

The previous work of the writer ('38, '39) and the investigations reported here have demonstrated that: The grouping of goldfishes produces a group effect that is manifested by the decreased activity of grouped individuals compared with isolated ones. Vision is the primary sensory modality involved in the phenomenon. The visual response is to form.

When *C. auratus* is grouped with other species, the visual response to form does not induce a group effect.

It is seen that the results of Escobar, Minahan, and Shaw ('36) on the activity of *C. auratus* in heterotypic groups is confirmed in that there is no group effect in heterotypic combinations. However, their data indicate that a goldfish in a heterotypic group is even more active than in isolation. While they do not give statistical analyses, there is a possibility that the difference is significant. This might indicate that the usual effect in homotypic groups is reversed so that the goldfish is more disturbed by the presence of certain species than it is by isolation.

The data in the experiments reported here do not lend themselves very well to cross-comparison. Spencer ('39) measured the activity *per se* of *C. auratus*. He found that individual activity patterns may be superimposed upon a species pattern. He also found certain cycles in activity. Our data also indicate a marked individual variation in locomotor activity. When more than one experiment was conducted at a time, the individuals used in the various set-ups were different. It is safest, therefore, to make comparisons within an experiment between the control and the experimental states.

It is desirable, however, to analyze the data to see whether the test goldfish is more active in a heterotypic group than it is in isolation. The total mean activity of an isolated test goldfish is represented by the control condition in *A* and *B* of table 3 and *A, B,* and *C* of table 4. The total mean activity of a test goldfish in actual contact and in visual contact alone with other species is represented by the heterotypic condition in *B* and *C* of table 1 and by the experimental condition in *B* and *C* of table 4. *A* of table 1 was not used in the comparison because this experiment was performed upon a different set of fishes in a different volume of water at Chicago. The heterotypic group in *D* of table 1 was a "modified" one inasmuch as it contained another

goldfish in addition to the experimental one and hence was not used. *A* and *B* in the experimental condition in table 3 were not employed inasmuch as they involved artificial models and we are concerned with actual species, living or mounted. Finally, *A* of table 4 in the experimental state was not used as in this case the group consisted of three goldfishes in addition to the experimental one.

Combining mean activities we find a total of 315.1 for the isolated *C. auratus* and 326.2 for a goldfish in actual contact or in contact through vision alone with other species. There is no statistical significance. Thus, the data in these experiments indicate that the activity of *C. auratus* is the same in isolation as it is in heterotypic groups, at least as far as tested. By the same token it is demonstrated that the heterotypic grouping employed did not merely reduce the intensity of the homotypic group effect but actually eliminated it.

It will be noted that the mean activity in the experimental states in tables 5 and 7, while significantly higher than the controls, is considerably and probably significantly below the total mean activity of 315.1 for an isolated goldfish. Thus, it may be concluded that while the fan-tail variety is not as effective in producing a group effect on common comets as are other common comets, it does act to diminish activity. It would be interesting to use various other species approaching a goldfish in form to determine if there is a "threshold" for this group effect. Obviously, all factors but form would have to be eliminated.

While the evidence has indicated that visual response to form is the major factor in the group effect in the goldfish, the rôle of movement cannot be completely dismissed. In the first place, only a small number of species have been tested. Additional experimentation may reveal that species that differ from the goldfish in contour but approach it in the type of swimming movement will produce the group effect. It may be argued that al-

though response to form is indicated by mounted specimen tests, it is superseded by response to movement in free-swimming groups. An experimental procedure that might profitably be used here would be an attempt to change the form of a free-swimming common comet without changing the type of swimming movement. In *C* of table 4, it is possible that the isolated goldfish in visual contact with mounted *A. portalegrensis* not only is less active due to the different form of these cichlids but in fact, in the absence of movement in these forms, fails to recognize them as fishes. However, it must be remembered that movement is not necessary to induce a group effect if the mounted forms are goldfishes.

Much of the investigation involving the reaction of fish to fish has been in experimental behavior studies on sex recognition and sexual selection. Sexual behavior is often striking and in a way more easily investigated as behavior patterns are less subtle than those involved in the aggregational tendency of fishes that are not definitely schooling forms. Also, factors that are dominant in sex reactions of fish to fish may not be involved at all in schooling or aggregating reactions. The latter, exemplified by the group effect in goldfishes, require considerable data and statistical analysis. However, considering the many qualitative and subjective aspects of sexual behavior studies, they too would not suffer if statistical treatment were applied wherever possible.

Many sexual behavior studies emphasize the importance of movement *per se* or of a particular type in sexual recognition. Breder and Coates ('35) find that degree of activity and movement are important in stimulating mating activity in male *Lebistes reticulatus*. No sex-recognition as such was found. Breder ('36) working with *Lepomis auritus* and Noble ('34) with *Eupomotis gibbosus* found that males would attempt to mate with a variety of objects irrespective of their general appearance provided they

were so manipulated as somewhat to resemble the actions of a female ready to spawn. In his review of sexual selection in fishes, Noble ('38) indicates the greater importance of movement than color or form in breeding behavior. The importance of movement in the breeding and schooling behavior of *Hemichromis bimaculatus* is reported by Noble and Curtis ('39).

The importance of differential behavior manifest through movement in the sexual behavior of fishes is not too unexpected. Most investigators agree on the importance of vision as the primary sensory modality in the general and especially sexual behavior of most fishes. Since form, in general, remains constant during adult life and nuptial adornment does not occur in many species, differential movement would be indicated as an important factor. On the other hand, many field observations emphasize the rôle of form *per se* or of a particular type in inducing schooling or aggregating reactions.

Granted that the group effect in *C. auratus* is a result of visual response to general goldfish body form, it is interesting to speculate whether the behavior pattern is learned or innate. Noble ('38) states that *Lebistes reticulatus* reared from birth with another species (*Mollienisia sphenops*) will not school with this species but with their own kind when given an opportunity. In spite of this inherited tendency to keep with their own kind, male guppies reared in isolation will attempt to mate with a great variety of small fishes introduced into the tank. Thus, it is indicated that for this species schooling is an innate response and sex recognition a learned one. Noble and Curtis ('39) find that *Hemichromis bimaculatus* reared alone or with other species schools with its own kind upon the first encounter. This species is also found to hatch with a greater interest in moving red disks than in black, blue, or yellow ones. The inherited preference may be modified by training, however, though it is never completely lost.

It would be interesting to rear *C. auratus* in isolation and subsequently investigate its various behavior patterns. The innateness of the visual response to form could be tested by rearing with species differing distinctly in form and then placing them with free-swimming goldfishes or in visual contact with mounted individuals of the same species.

Lorenz ('37) states that most birds do not recognize their own species "instinctively" and often some or all of a bird's social reactions can be released by other than their normal object. It is found that, during a brief and very definite period in the life of the young bird, the process of acquiring the "right" object of social reactions by conditioning it to the species as such must take place and this is called *imprinting*.

There is quite a gap phylogenetically between the fishes and birds but much recent experimentation indicates a parallelism in certain aspects of behavior, especially those involved in breeding. Many fresh-water fishes establish territories. Social hierarchies involving "pecking orders" are well-established in many birds; Noble and Borne ('38) report straight line pecking orders in the sword-tail, *Xiphophorus hellerii*. Thus, it is possible that many of the implications made by Lorenz ('37) may be profitably investigated in fishes.

Any analysis of the behavior of heterotypic groups may be important since such aggregations have ecological implications of far-reaching significance in the study of animal communities in nature. As Allee ('31, p. 87) points out . . . "a decided advance toward social life is made by the appearance of tolerance for other animals in a limited space. . . ." Thus, a heterotypic collection of fishes in an aquarium may serve as a social microcosm. Although the investigations reported here do not indicate any group effect on *C. auratus* when placed with other species, there is a state of "tolerance" as indicated by locomotor activity. That is to say, in general, goldfishes are not more active in the heterotypic groups studied than they are in isolation. This tolerance is not learned but is innate inasmuch, as far as is known, the specimens of *N. rubrifrons, A. portalegrensis, Barbus partipentazona* (?) and *X. hellerii* had never been grouped with *C. auratus* before.

Sight, the primary sensory modality in the social behavior of fishes, plays an important rôle in the organization of many other groups, *i.e.*, vultures, male frogs in the breeding season, young catfishes, and fireflies (Allee, '31, p. 89, 90). No less important, however, is the analysis of the components of that sensory reaction system, namely response to form, color, type of movement, and amount of movement. It is of course possible, as "emergent evolution" implies, that the whole is greater than the sum of its parts. Obviously, however, this cannot be determined, if indeed it ever can be, considering the complex nature of the subject, without a knowledge of those parts. An indication of the complexity of such animal behavior studies is given by Noble and Curtis ('39). They find in *Hemichromis bimaculatus* that nuptial colors *per se* are not attractive to the female but serve to render both the sex identifying and the sex stimulating movements of the male more conspicuous. Thus, one of the parts in the whole is superimposed upon another.

SUMMARY

1. It has been found that a goldfish is less active when placed with others of its kind than it is when isolated. This homotypic group effect is lost when *C. auratus* is grouped with different species or with stationary sunfish models; it is also lost when a goldfish is in contact through vision alone with other free-swimming or mounted species or with sunfish models.

2. If the heterotypic group contains one goldfish in addition to the experimental animal, the group effect is maintained.

3. When members of a different variety of *C. auratus* are grouped with the experimental variety or are placed in visual contact with them as mounted forms, the group effect is appreciably diminished but not lost.

4. Visual response to a goldfish-like form is apparently the major factor involved.

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# FROST HEAVING AND DAMAGE TO BLACK
## LOCUST SEEDLINGS

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In the spring of 1936 a study was initiated to determine the extent of frost heaving of black locust (*Robinia pseudacacia* Linn.) which had been planted during the preceding winter. The areas studied were in the Tennessee River valley of northern Alabama, in Lawrence, Limestone, and Madison counties. Altogether 10 plantations were studied, and counts were made of nearly 4,000 seedlings.

The winter of 1935–1936 stands out as one of the coldest the South had experienced in many years. In northern Alabama the winter was more severe than any of the present century except the winter of 1917–1918, according to the United States Weather Bureau substation at Madison, Madison County, Alabama. During the winter of 1935–1936 there were seventy-one days when the minimum temperature was 32 degrees Fahrenheit or lower, with a season's low of 5 degrees below zero. By subtracting those days in which the temperature did not go below 32 degrees, and by omitting also those in which the temperature did not rise above the freezing point, there still remained fifty days in which the temperature fluctuated close to the freezing point. It is probable that in most of these fifty instances sufficient frost action occurred to cause some lifting of newly planted seedlings.

The study of frost heaving of black locust seedlings was made on the basis of three variable factors, namely: planting site conditions, size of seedlings, and time of planting. In studying the effect which planting site conditions had on frost heaving the site conditions were divided into five separate categories. These five classifications, combining both ground cover and erosion conditions, were as follows:

1. *Sodded areas,* where the plant cover was sufficient to prevent any erosion. The sod of broom sedge or other plant growth was thick enough to make it necessary to scalp a spot for planting each seedling.

2. *Sheet eroded areas,* where plant growth existed, such as wire or crab grass, but where it was too thin or too scattered to prevent sheet erosion.

3. *Gullied areas,* where the land was devoid of any plant growth, and where erosion was very active. Most of these gullies were from 5 to 10 feet deep, and the sides sloped at approximately a 45 degree angle.

4. *Matted areas;* those gully banks which were sloped according to engineering specifications, and which were mulched with hardwood or cedar brush.

5. *Poorly matted areas,* which received the same treatment as under No. 4, but in which the mulch was not properly replaced around the seedlings after they had been planted. When the seedling was in the middle of a square foot of unmulched soil it was considered to be improperly protected.

In selecting the areas to be studied only those plantings which furnished two or more of the above mentioned classifications were chosen. This assured comparable results, and was the only check possible. The effect which size of planting stock had on heaving was separated according to the three sizes of seedlings which were used during the season; that is, small, medium, and large seedlings as represented by plants 6–12 inches, 12–18 inches, and 18–24 inches tall, respectively. Correlation of frost heaving with time of planting was made for those plantations established in early winter and in the spring.

Figure 1 depicts the percentages of
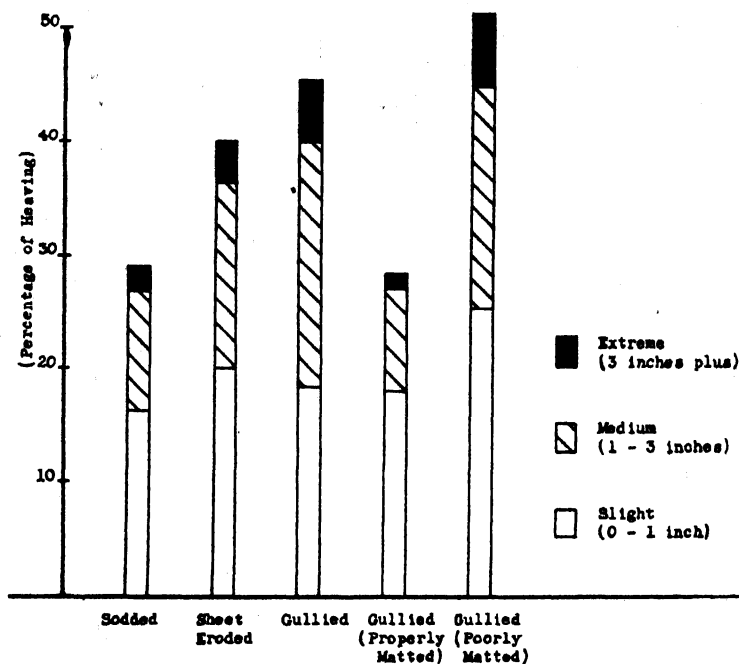
Fig. 1. Frost heaving of Black Locust seedlings for varying site conditions (Tennessee River valley, northern Alabama, winter of 1935–1936).

seedlings that were heaved by frost action for each of the five ground-cover classifications; these were 28.5, 38.5, and 45.2 per cent, respectively, for all seedlings planted on sodded, sheet eroded, or gullied areas. For those gullies which received engineering and mulching treatment frost heaving was 28.3 per cent for the properly matted and 51.3 per cent for the improperly matted areas. It is interesting to note that both the properly matted and the sodded areas afforded practically the same protection to the seedlings, even though the protection in the one instance was furnished by artificially placed vegetation on a severely eroded site, and in the other by natural growth on a site where erosion was stabilized. On the other hand, trees planted on improperly matted areas suffered somewhat more than did those planted on barren, unworked, gullied areas, although this increase is not very significant. The important point is that an improperly matted area gave no better protection to newly planted seedlings than did severely eroded

but unmulched areas. In addition, frost heaving on such sites totaled nearly twice as much as on the properly matted areas, and was over six times as great when considering only that group' that was lifted three inches or more. It seems evident, therefore, that if mulching is to be properly used it must be properly placed.

It was found that the size of the seedlings had a noticeable effect on the amount of frost heaving. Frost action affected an average of 50 per cent of the small (6–12 in.) plants, 46 per cent of the medium (12–18 in.) plants, and 33 per cent of the large (18–24 in.) plants. These comparisons were for sheet eroded areas only.

Frost action as it affected fall or early winter planted seedlings was only slightly different from that of spring planted seedlings. Small seedlings planted in late November or early December had an average heaval of 53 per cent compared to 48 per cent for those planted in the spring. Medium sized plants showed 47

per cent for fall against 45.5 per cent for spring plantings, and large plants showed 34 per cent compared to 32 per cent. These comparisons were all made on sheet eroded areas, although a few measurements made on other type lands showed approximately the same relationship. These figures are all the more astonishing when it is realized that fall or early winter plantings had an average of forty-two days in which freezing action could take place, whereas spring plantings had only five such days. In the case of the fall plantings, the planting date was followed immediately by several successive freezing and thawing days, whereas the spring plantings had only two immediately after planting, followed by three others each spaced a week apart.

Inasmuch as the variation in heaving of winter planted seedlings as compared with spring planted seedlings was not greater than 5 per cent, and since the winter planted stock was followed by an average of forty-two days in which freezing and thawing action occurred as against five after spring planted trees, it seems logical to assume that frost heaving of black locust was not cumulative beyond a certain point. Now, since the five days of freezing and thawing action which followed the establishing of the spring plantations occurred within a period of three weeks it seems that the point beyond which frost heaving was not cumulative was certainly not more than three weeks, and probably not more than two weeks. This latter figure is mentioned because frost action during the first two weeks following planting operations in the winter was considerably more severe than that of the three weeks which followed spring planting, and yet the results of the two periods were very similar. Whether this cessation on frost heaving after a two- or three-week period was the result of the packing of the soil, whether it was caused by root growth after planting, or whether it was a combination of the two was not determined. It is the writer's opinion that it was a combination of the two; this opinion being based on the fact that root growth of hardwoods is known to occur after the foliage has been dropped in the fall and again before the buds open in the spring, and also on the fact that frost action could not have penetrated more than five or six inches of ground, thus giving the soil around the lower part of the root system a chance to become firm and compact. This latter reason probably explains why the larger plants did not suffer as severely as did the smaller ones on similar sites.

The mortality of black locust seedlings which could be attributed directly to frost action would not be greater than the percentage of those seedlings which were heaved almost or completely out of the ground (see fig. 1). This would average not more than 5 per cent. Actually, not all those seedlings would die, because many of them would still have enough of the root system established to continue a precarious existence. Of those seedlings that were raised less than 3 inches by freezing few had died, and apparently none of the deaths was caused by the frost action. Other damage which would be caused as a result of heaving would be a reduced growth rate due to the fact that part of the root system was raised into the air, and also to the probability that part of the roots might have been injured. This retarding effect on growth, though, would probably be temporary, lasting only until a complete root system had been re-established below ground.

SUMMARY

The extent of frost heaving and damage to black locust seedlings as shown by this article, due to the severity of the winter of 1935–1936, can be considered as the maximum which will result in any of the Southern States.

Protection to seedlings against frost heaval was in direct proportion to the ground cover. Seedlings planted in stabilized sites with sufficient vegetation and barren gullies which were properly

mulched were nearly equally protected, whereas seedlings in severely eroded gullies, or in similar areas when improperly mulched, were almost equally damaged.

Frost heaval of seedlings was in an inverse proportion to seedling size, affecting approximately one-third of the larger plants and approximately one-half of the smaller ones.

The effect of frost action on both winter and spring planted seedlings was nearly the same, from which fact it is inferred that frost heaving was not cumulative. It further appeared that in approximately two weeks the plants were stabilized against further freezes, either by root growth, soil settling, or a combination of the two.

Damage to black locust seedlings resulted in mortality to not over 5 per cent of the stand, and in a probable decreased height growth for a period of time not longer than necessary for the plant to re-establish a balanced root system.

# NOMOGRAMS FOR THE CONVERSION OF PSYCHROMETRIC DATA INTO EXPRESSIONS OF VAPOR PRESSURE, DEW POINT, RELATIVE HUMIDITY, OR VAPOR PRESSURE DEFICIT

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The repeated solution of more or less involved equations by actual computation, with or without the use of tables, is being advantageously replaced in many fields by mechanical solution through the use of nomograms. In these devices the mathematical equation that defines the relationship existing between a set of variables is represented by a geometric pattern on a plane surface, one scale line in this pattern being constructed for each variable in the equation. The equation itself may then be solved for any one unknown by laying a straight-edge in appropriate positions across the pattern and thereby reading off the answer without any arithmetic calculation whatsoever.

In the ecological field, pertinent application of this time-saving principle may be made for the conversion of basic psychrometric measurements of humidity into their various alternative forms of expression, or the conversion of any of these expressions into another form more suitable to a problem at hand. Two nomograms are presented herein to meet this need.[1] While they were designed primarily for the direct conversion of wet and dry bulb psychrometer readings into the corresponding vapor pressure, dew point, relative humidity, and vapor pressure deficit values, they may also be used for conversions within the latter group of alternative expressions.

The nomogram in figure 1 is a graphic portrayal of the equations relating dry and wet bulb psychrometer temperatures, vapor pressure, dew point, and relative humidity for the barometric pressures of 30, 29, 27, and 25 inches. The use of

[1] Reconstruction of these nomograms with Fahrenheit scales is planned for the near future.

the nomogram is illustrated by the following example. In a region where the average observed air pressure is about 29 inches, dry and wet bulb thermometer readings of 30° C. and 20° C. respectively, have been obtained. A straight edge, preferably a transparent one, connecting these respective values on the 29-inch dry and wet bulb temperature scales cuts the vapor pressure scale at 12.5 mm., the corresponding vapor pressure reading. To secure the equivalent relative humidity, an additional operation is necessary. A straight-edge connecting 12.5 mm. on the vapor pressure scale, and 30° on the oblique dry bulb temperature scale cuts the relative humidity scale at approximately 40, the corresponding percentage relative humidity.

Any one of the expressions represented in this nomogram may be secured when two occurring on different axes are known. It must be noted, however, that the common axis for dew point and vapor pressure is the connecting link between the vertical dry and wet bulb temperature scales on one hand, and the relative humidity and oblique dry bulb temperature scales on the other. It is not possible in this nomogram to derive relative humidity directly from wet and dry bulb temperatures, nor is it possible to derive wet bulb temperature directly from relative humidity and dry bulb temperature without in either case pivoting upon the axis for dew point and vapor pressure.

Figure 2 is a nomographic representation of the equations connecting dry and wet bulb psychrometer temperatures with vapor pressure deficit for atmospheric pressures of 30, 29, 27, and 25 inches. Vapor pressure deficit in each case is derived directly by connecting,
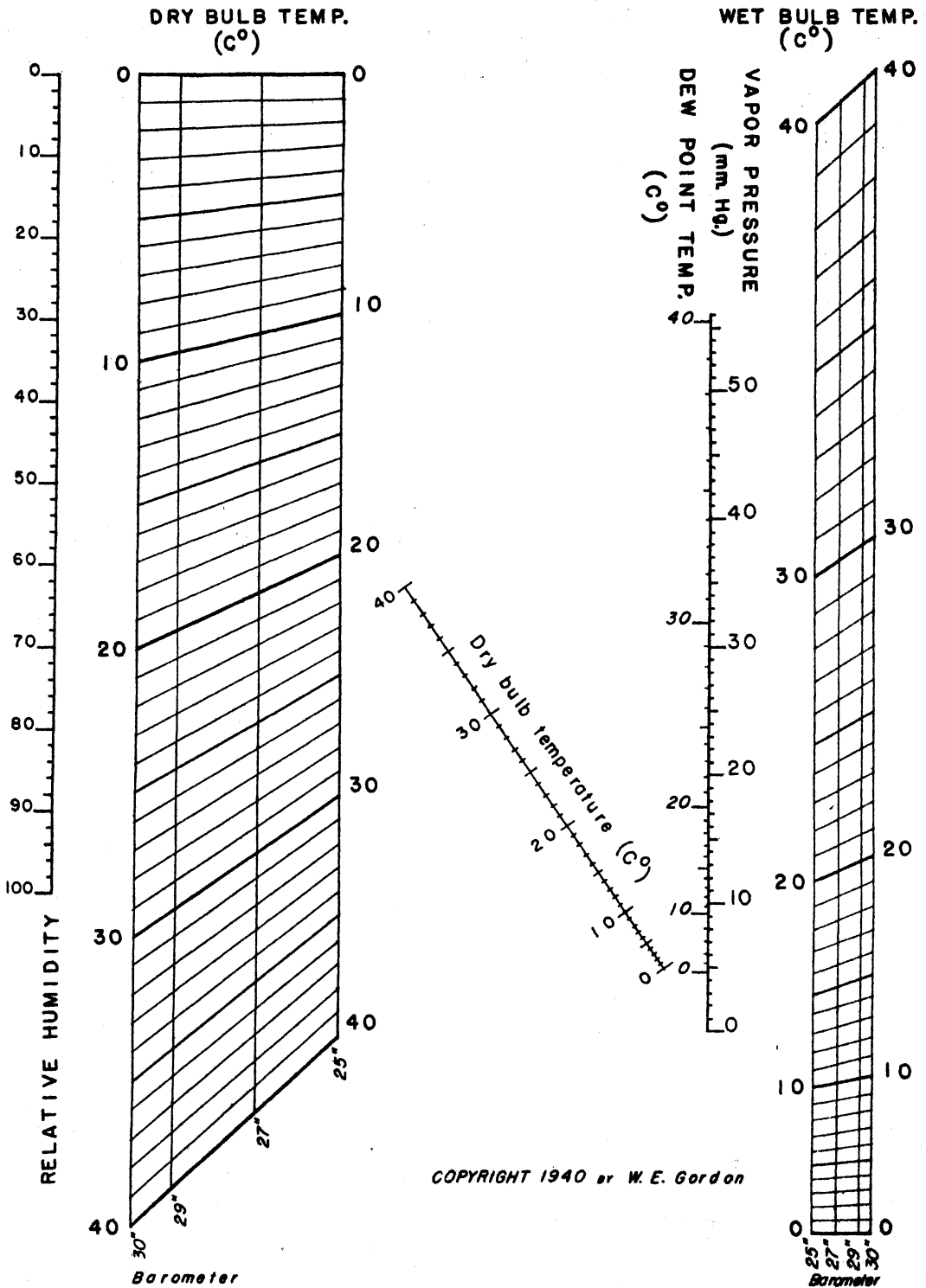
FIG. 1.  Nomogram for the conversion of wet and dry bulb temperatures to vapor pressure, dew point, and relative humidity at barometric pressures of 30, 29, 27, and 25 inches.
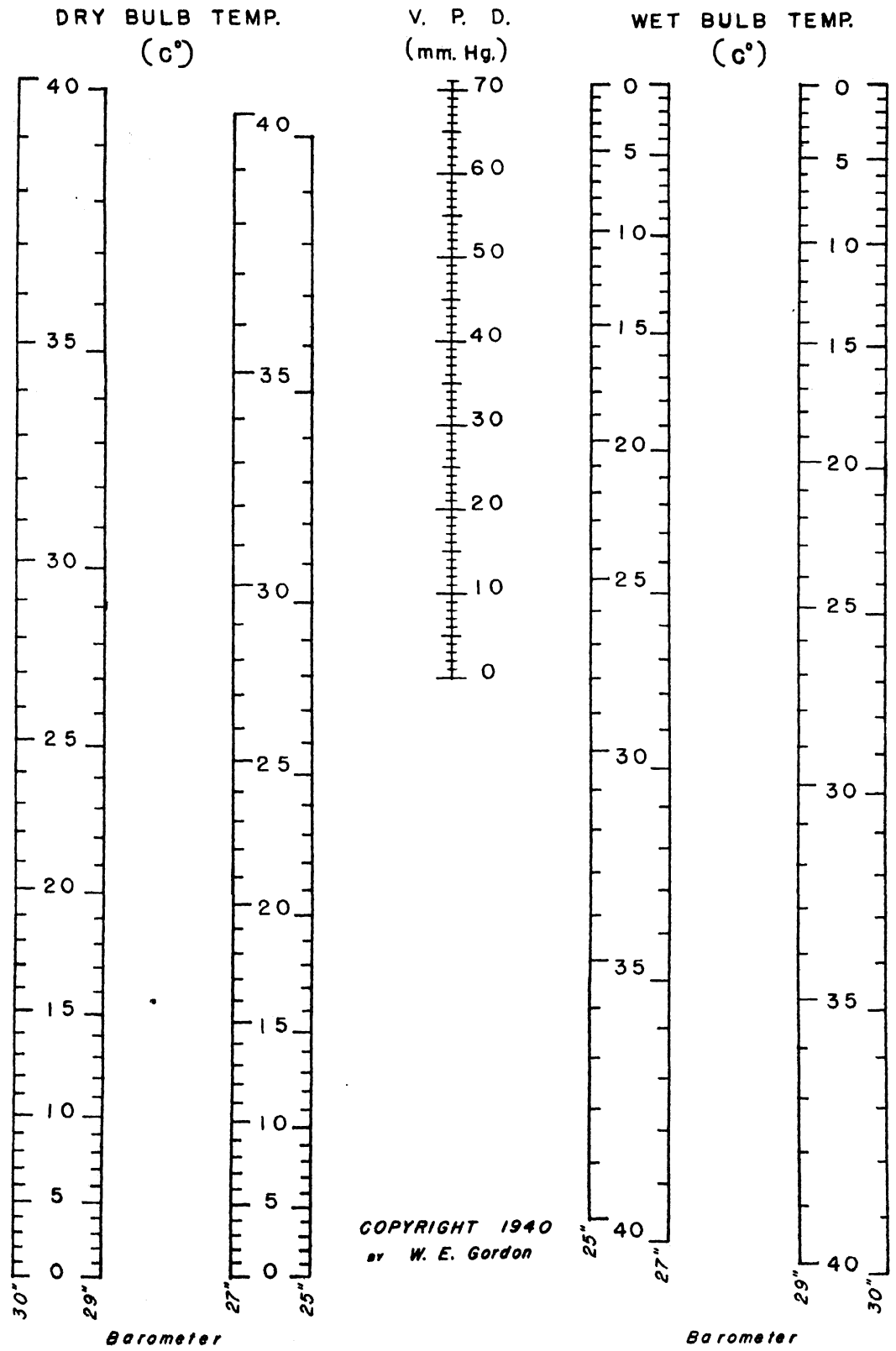
FIG. 2.  Nomogram for the conversion of wet and dry bulb temperatures to vapor pressure deficit at barometric pressures of 30, 29, 27, and 25 inches.

with a straight-edge, the respective psychrometer readings on the proper pressure axes. The intersection of this line with the vapor pressure deficit scale yields the appropriate value on that scale. Thus with an atmospheric pressure of 30 inches, and dry and wet bulb readings of 30° and 20° respectively, a straight-edge connecting these values cuts the vapor pressure deficit scale at 19.5 mm., the desired value.

Limitations in the accuracy of results obtained by the use of a nomogram are primarily functions of the size of the nomogram and the care with which it is used. In particular, care must be taken to connect the temperature values on axes representing the same barometric pressure. Failure to do this will seriously distort the results obtained. Interpolations in the nomograms presented here are practical to the nearest half unit in all cases, and in some portions of the scales to the nearest one-fifth unit. Both nomograms have been constructed to give exactly correct expression to the psychrometric formula [2] when the difference between the dry and wet bulb reading is 10°. In the simplification of the equations involved, a systematic error of approximately 1 per cent in the extremes of wet and dry bulb difference was unavoidably introduced. Thus, with depressions of less than 10° there is a slight positive error in the vapor pressure deficit nomogram, while with depressions of the wet bulb greater than 10° there is a slight negative error. In the nomogram for vapor pressure the errors are of the same magnitude in the reverse order. This error is felt to be well within the range of experimental error normally experienced in the use of the psychrometer.

It is hoped that vapor pressure deficit, which can now be computed in a single operation directly from wet and dry bulb psychrometer readings, will receive a wider application in ecological work, supplanting in particular the use of relative humidity. In spite of criticism of the use of vapor pressure deficit recently made by Thornthwaite,[3] there is at present no adequate substitute for it of comparable value in estimating the influence of atmospheric humidity on the water balance of the plant. Thornthwaite correctly points out that the quantity of water evaporated from soil and water surfaces, the temperatures of which do not follow closely that of the atmosphere, may be quite independent of the magnitude of the vapor pressure deficit of the atmosphere above those surfaces. However, with respect to small, free evaporation surfaces, the temperatures of which do follow rather closely that of the atmosphere, very high correlations have been demonstrated between the rate of water removal and the intensity of the "water-removing" factor as expressed by empirically combined measurements of wind and vapor pressure deficit. Furthermore, the intensity of this factor, to be of importance to the plant, need not result in a definite or predictable quantity of water lost by evaporation. Rather, in many ecological problems, it is of interest chiefly as it influences the physiological behavior and the anatomical development of the plant. The demonstrated usefulness of vapor pressure deficit in this connection makes it desirable to retain this practical expression until an alternative is available which satisfies theoretical requirements more fully without substantial loss in ease of determination.

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[2] Prof. Ferrel's formula as given in *Smithsonian Meteorological Tables*, 5th ed., p. lxix (1931) was used.

[3] **Thornthwaite, C. W.** 1940. Atmospheric moisture in relation to ecological problems. *Ecology* 21: 17–28.

# NOTES AND COMMENT

## A METHOD FOR OBTAINING CONTINUOUS RECORDS OF DISSOLVED OXYGEN IN LAKE WATERS [1]

Recently it has been shown that the dropping mercury electrode is applicable to the determination of dissolved oxygen. Thus far, its use for oxygen determination has been confined to laboratory measurements of photosynthesis and respiration (Petering and Daniels, '38; Petering, Duggar and Daniels, '39; Blinks and Skow, '38). Its favorable behavior in laboratory studies has indicated that it may be feasible to use the dropping mercury electrode in natural waters, such as lakes and streams, for the direct determination of dissolved oxygen, and particularly for measurement of changes in dissolved oxygen concentration. The results presented below were obtained at Trout Lake in northern Wisconsin, and indicate that this application of the dropping mercury electrode should prove to be very valuable.

### APPARATUS

When a potential of approximately one volt is impressed on a dropping mercury electrode cell containing an aqueous solution of oxygen, the resulting current flow is due principally to the reduction of oxygen at the dropping mercury cathode. Other conditions remaining constant, the rate of diffusion of oxygen to the mercury surface is proportional to the concentration of dissolved oxygen in the immediate vicinity of the cathode. Consequently the amount of current flowing is approximately proportional to the concentration of dissolved oxygen. The method as developed by Petering and Daniels ('38) is essentially an empirical one, and requires calibration by suitable absolute determinations (Winkler method).

Any other materials in solution having decomposition potentials in the same range as oxygen will interfere with the oxygen determination unless they are removed or corrected for. However, if the concentration of interfering substances remains constant, changes in oxygen concentration may be accurately measured. Hence, the method is particularly suitable for following changes in the concentration of dissolved oxygen at a fixed location.

The preceding paragraphs represent a considerable over-simplification of the principles involved; more complete discussions are given by Kolthoff and Lingane ('39) and by Petering and Daniels ('38).

In laboratory experiments, Petering *et al* re-

corded the difference in galvanometer deflection between 0.1 and 1.0 volt potentials as a measure of dissolved oxygen. In part, the small current flowing at 0.1 volt is due to the presence of traces of easily reducible substances, and their effect would be eliminated by using the difference between 0.1 and 1.0 volts to represent oxygen. This procedure was not feasible with the apparatus available for the present work, where a continuous record was desired. Fortunately, the 0.1 volt reading was not found necessary in these experiments, since the 0.1 volt deflections were found to be small compared with the 1.0 volt deflections, and constant within the accuracy of measurement.

In using the dropping mercury electrode for determining changes in oxygen concentration, it is necessary either to maintain a constant temperature, or to have an accurate record of temperature changes, since the amount of current produced for a given concentration of oxygen is a function of temperature. Because temperatures in natural waters are not constant, even for brief periods, it was necessary to include in the apparatus a device for recording temperature variations in the immediate vicinity of the electrode. A resistance thermometer, previously constructed by Dr. L. V. Whitney, was used for this purpose.
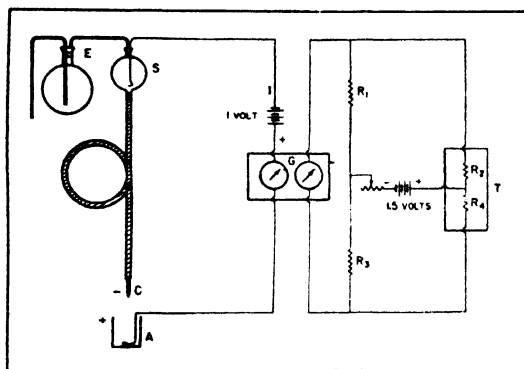


FIG. 1. Diagram of electrode and thermometer circuits.

Figure 1 shows, in diagrammatic form, the essential features of the entire apparatus. A Cambridge recorder (*G* in fig. 1) with two galvanometers, each having a sensitivity of approximately one scale division per microampere, provided a 24-hour record of the galvanometer deflections produced by the current flowing in the thermometer and electrode circuits.

The dropping mercury electrode circuit is shown on the left in fig. 1. The 1.0 volt potential was supplied by a storage battery and resistances, and frequently checked against a potentiometer circuit not shown in the diagram. A heavy, two-wire, rubber insulated cable connected the galvanometer and source of potential with the remainder of the electrode apparatus, which was attached to a rigid post driven into the lake bottom where the water depth was approximately one meter. "S" in fig. 1 is a glass reservoir (approximately 200 ml. in this case) containing mercury. The negative lead wire terminated in "S," with the mercury in the rubber connecting tube serving to complete the circuit to the glass capillary "C." The tip of this capillary constituted the dropping mercury cathode. With the particular capillary used in these experiments, a pressure head of about 80 cm. was necessary to obtain a drop rate of one drop in 1.5 seconds. The drop rate was usually found to remain constant during periods of 24 hours or longer. The rate of mercury flow was of the order of one ml. per hour. The mercury droplets were caught in the anode vessel "A," which was the terminus of the positive lead wire. The distance between "C" and "A" was made sufficiently large (about 10 cm.) to permit free circulation of water about the capillary tip. "E" in fig. 1 is an air reservoir which permitted the maintenance of a constant pressure difference between "S" and "C" (except

for the slowly changing mercury level in "S"), without permitting water to enter "S."

The right hand portion of fig. 1 shows the thermometer circuit, which is in effect an unbalanced Wheatstone bridge. The thermometer "T" consisted of a thin, water-proof brass jacket, containing the two approximately equal resistances $R_2$ and $R_4$, which were constructed of metals having different temperature coefficients of resistance. A three-wire insulated cable connected the rest of the circuit with the thermometer, which was placed within a few centimeters of the capillary electrode tip. The thermometer was calibrated against a mercury thermometer, and was found to give a linear response within the desired temperature range.

## RESULTS

The upper curve in fig. 2 shows, in original form, a 24-hour record of deflections due to dissolved oxygen. During this period (July 26–27, 1939) the dropping mercury cathode ("C" in fig. 1) was kept at a depth of 0.5 meters below the surface of Trout Lake. Temporary interruptions in the rate of mercury flow were responsible for the occasional points scattered below the curve. Laboratory studies have shown that cathode tips with somewhat larger capillaries than the one used in these experiments usually give more regular rates of flow.

The lower curve in fig. 2 shows the tempera-
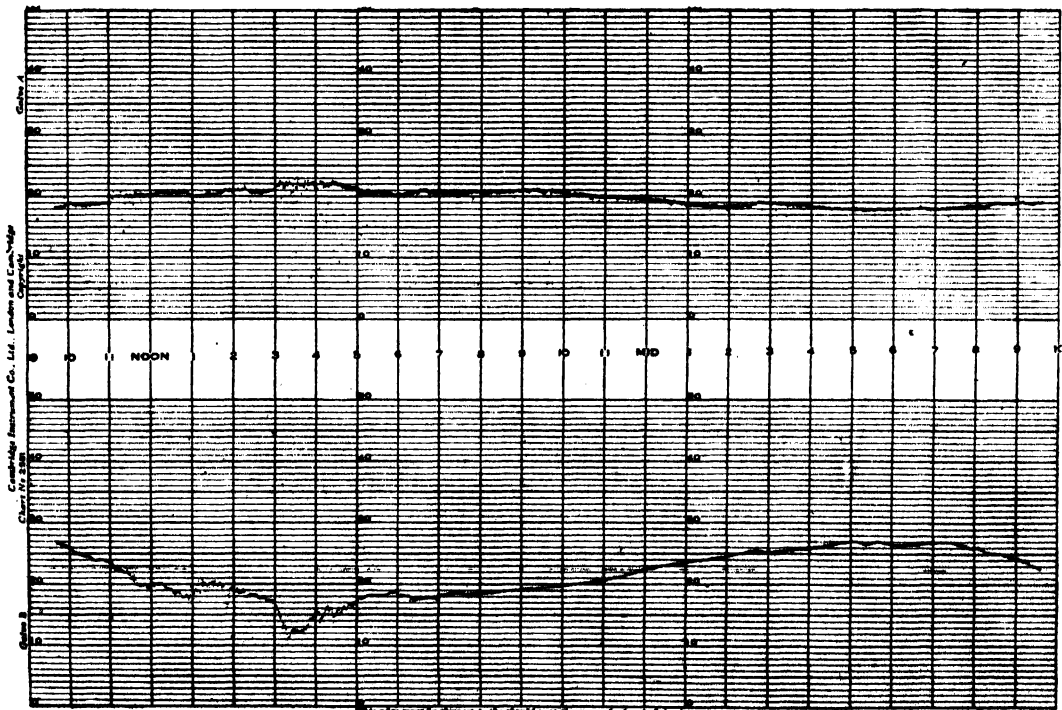


FIG. 2.  24-hour record of electrode and thermometer currents.

ture record corresponding to the oxygen record shown in the upper curve. The circuit was arranged so that an increase in temperature gave a decrease in thermometer current.



A—TEMPERATURE
B—SOLAR RADIATION
C—DISSOLVED OXYGEN
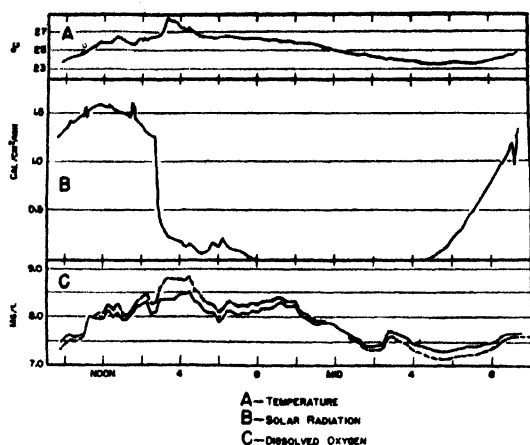
FIG. 3. Derived curves for temperature, solar radiation and oxygen variations.

Figure 3 is derived from fig. 2, except for the solar energy record (*3B*), which was obtained from another recorder and included to show the effect of solar radiation on both temperature and oxygen. Fig. *3A* shows the actual temperature variation at the point of observation in the lake and *3C* shows the variations in dissolved oxygen. In both cases the curves are drawn on the basis of points taken from fig. 2 at intervals corresponding to 15 minutes or less. The solid line in fig. *3C* represents the actual oxygen variation, while the dotted line corresponds, except for scale, to the deflections shown in fig. *2A* and is uncorrected for temperature changes, since it assumes the temperature to be constant at 25° C. The temperature correction used to obtain the solid line in fig. *3C* corresponds to a temperature coefficient, for galvanometer deflection, of 1.6 per cent per degree C. This value is based on results obtained by Dr. H. G. Petering and by Mr. W. E. Moore, working independently in the Botany Department at the University of Wisconsin. The absolute values of dissolved oxygen are based on a calibration of the electrode by means of the usual Winkler method of analysis.

Atmospheric conditions during the period of measurement were such as to favor the development of the rather abrupt changes frequently shown in both the temperature and the oxygen curves. The air temperature was high on July 26, the sky was clear until mid-afternoon, and the wind was intermittent, never being strong enough to produce real waves. The water currents were thus insufficient to produce a homogeneous layer in the upper meter of water, but

sufficient to cause frequent replacement of the water in the vicinity of the electrode.

Despite the frequent abrupt variations shown in fig. 3, there is also evident in both the oxygen and temperature records a distinct diurnal trend which correlates with the solar energy record. The general effect due to photosynthesis and respiration is clear, even though the plankton population in Trout Lake at the time of measurement was quite sparse.

In other experiments, the dropping mercury electrode was suspended from a buoy about 300 meters from shore. The electrode gave good results at various depths whenever the lake was calm. But in rough weather, the mechanical disturbance of wave action on the buoy interfered with the formation of mercury drops at the capillary tip, and the resulting variations in current flow made accurate measurements impossible. For this reason, the use of the electrode for measuring oxygen changes is apparently limited to locations where the electrode may be held rigidly, or to calm waters (*e.g.* ponds or small lakes).

### APPLICATIONS

Several possible applications of this method are evident. Perhaps the most valuable, from a strictly limnological point of view, will be its application to studies of lake productivity. Heretofore, such studies have necessitated the measurement of photosynthesis and respiration of lake waters in closed glass bottles. The presence of glass surfaces greatly stimulates bacterial growth. During long exposures, the increased bacterial growth may influence the total amount of both respiration and photosynthesis. The method described in this report will permit such measurements to be made continuously and directly in the natural environment, which is a very distinct advantage over the earlier method.

Continuous oxygen records may also prove valuable in pollution studies, or in other cases where temporary depletion of oxygen may be a serious problem.

### SUMMARY

A dropping mercury electrode is described which can be immersed in a lake or stream and connected with a recorder on shore to give a continuous record of changes in dissolved oxygen concentration.

Wisconsin in making available part of the apparatus used in this investigation.

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## ALACHUA COUNTY, FLORIDA, SOILS AND VIOLETS

The soils of Florida have developed mainly from limestone, marls, and marine deposits of sands and clays. In the central part of the state limestones have weathered to form the parent materials of the Gainesville, Hernando, and Fellowship soils. The limestone deposits are usually buried beneath more recent deposits of sands, clays, marls, and organic matter. Sometimes, however, the limestone is near enough to the surface to influence directly the character of the soil and its vegetation.

Alachua County soils of calcareous derivation belong to the three groups mentioned above. The characteristic vegetation of the Fellowship series is hardwood timber, palmetto, and loblolly pine; of the Hernando series, hardwood or longleaf and slash pines with wiregrass; and of the Gainesville series, hardwoods (mainly red oak), with some longleaf and loblolly pine. Soils derived chiefly from sands are represented in the county by the Norfolk and Orlando series. The former is widely distributed and supports large tracts of longleaf pine and turkey oak; the latter, found in the La Crosse area, is associated with longleaf pine and wiregrass, together with live-oak and bluejack oak. The flatwoods soils, known as "ground water podzols," have developed on marine deposits of noncalcareous sands. The Leon series, so abundant in Alachua County, supports longleaf and slash pines with an undergrowth of wiregrass, saw palmetto, and gallberry.

A study of the violets of Alachua County in relation to the soils in which they grow has recently been made by the author, the soil samples being analyzed by the Department of Soils of this Station. The species of violets are so nicely adjusted to their habitats that they serve as excellent indicators as is shown in the following list of local species with their habitats and soil requirements, arranged according to pH averages.

*Viola lanceolata* L. and *V. vittata* Greene. Common in wet or damp open ground, near slash pine or pond cypress, with pH about 5.1.

*Viola septemloba* LeConte. Common in low pinelands, associated with either slash pine or longleaf pine where the soil is damp, with pH about 5.1.

*Viola primulaefolia* L. Rather common in damp soil under longleaf or loblolly pine, usually near slash pines, with pH about 5.2.

*Viola villosa* Walt. Frequent in high, dry oak woods, especially under red oak and live-oak, growing in drier soil than any other local violet, with pH about 5.5.

*Viola esculenta* Ell. Frequent along streams under or near hardwood trees where the soil is sandy and damp, with pH about 5.75.

*Viola triloba* Schw. Common in high hammocks where the soil is rather dry with pH about 6.1.

*Viola walteri* House. Abundant in hammocks, ranging from dry to moist soil, with pH about 6.5.

*Viola floridana* Brainerd. Abundant in low hammocks, in either sandy or calcareous soil, with pH averaging about 6.9.

*Viola sororia* Willd. A northern species found in abundance in the bottom of a large lime-sink near Gainesville, where the pH of the soil is about 7.65.

On the basis of these studies it is now possible to predict which species of violets will be found in certain localities. If flatwoods are on the road ahead, *i.e.*, moist level tracts with slash or longleaf pine and occasional rain-water pools, one may expect white violets (*V. primulaefolia, V. lanceolata, V. vittata*) and the beautiful *V. septemloba;* if high hammocks, *V. triloba* and *V. walteri;* if red oak or dry live-oak woods, *V. villosa;* if moist hardwoods or low hammocks, *V. floridana* and *V. walteri;* and, if a flood-plain, *V. floridana* and *V. esculenta,* the

latter apparently better adapted to sand than to humus.

## SPECIFIC ECOLOGIC AMPLITUDE

The most ancient American types of violets are probably the woody forms found in the Andes. As regards local species, the three white-flowered ones represent an old group with low chromosome number (24) and few variations. As one would expect, they are adapted to a special fixed habitat, and exhibit an innate conservatism both morphologically and physiologically. *Viola walteri,* our only caulescent species, is also very constant in form.

The remaining local species, having a large number of chromosomes (54), are doubtless comparatively recent in origin and exhibit as a group an inherent plasticity. *V. triloba* and *V. septemloba* show a decided tendency to vary in leaf-form, while *V. floridana* varies in the size and color of flowers and has a rather wide soil and light range. The least plastic local member of this group appears to be *V. villosa,* which is here extremely restricted in habitat and constant in form. None of our local violets approach such plants as *Helianthus angustifolius* in ecologic amplitude.

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## A USEFUL METHOD FOR THE STUDY OF POLLEN IN PEAT

In the analysis of pollen in peat, it is necessary to free the pollen from adhering colloidal particles, and further it is frequently desirable to concentrate the pollen grains by separating them from other constituents of the peat. *Deflocculation* has been effected by various chemical reagents and by mechanical methods. One of the most widely used techniques in the past has been treatment with hot alkali, viz., 10 per cent aqueous sodium or potassium hydroxide or strong ammonium hydroxide. Similar results may be obtained by the use of 95 per cent alcohol at room temperature, or by vigorous mechanical dispersion. *Concentration* of the pollen has been secured either by sifting, layering or centrifuging, or by dissolving various constituents of the peat with strong mineral acids, boiling alkali and other substances. Various methods for the study and interpretation of pollen in peat have been summarized by Godwin.[1]

Recently we have been concerned with the analysis of a sedimentary marine peat which contains a relatively large percentage of inorganic constituents, diatoms, and sponge spicules, as well as pollen, spores, fungus hyphae, animal chitin, and fragments of plant tissues in different stages of decomposition. Many of the less involved techniques for pollen analysis as outlined by Sears,[2] Erdtman,[3] Geisler,[4] McCulloch[5] and others, were tried without obtaining entirely satisfactory results. It seemed desirable accordingly to determine whether some modification of the Cross and Bevan[6] (pp. 94–96; 134–137) technique for the purification of cellulose might not prove useful in the rapid deflocculation of peat and concentration of the pollen for critical study. Extensive use of the technique in the chemical analysis of normal lignified plant tissues and of humus has demonstrated that a series of brief chlorinations alternating with treatments with 2–4 per cent hot sodium sulphite are more effective for rapidly removing lignin, humic compounds and other substances—without degradation and loss of cellulose—than are one or two prolonged treatments with each of these reagents. It should be emphasized, in addition, that in chemical analyses of this type special pretreatments are utilized for the removal of fats, waxes, resins, and similar substances, since they are not dissolved by the dilute sodium sulphite following chlorination. Therefore, it appeared reasonable to anticipate that a large fraction of the organic constituents in peat might be effectively and rapidly extracted by a chlorine–sodium sulphite technique without loss of even the least resistant types of pollen.

The following schedule of treatments has yielded remarkably favorable results with the sedimentary peat which we have been studying:

[1] **Godwin, H.** 1934. Pollen analysis. An outline of the problems and potentialities of the method. *New Phytol.* 33: 278–305, 325–338.

[2] **Sears, P. B.** 1930. Common fossil pollen of the Erie Basin. *Bot. Gas.* 89: 95–106.

[3] **Erdtman, G.** 1935. Pollen statistics, a botanical and geological research method (in Wodehouse, R. P. *Pollen Grains,* pp. 110–125. McGraw-Hill Co.).

[4] **Geisler, F.** 1935. A new method for separation of fossil pollen. *Butler Univ. Bot. Studies* 3: 141–146.

[5] **McCulloch, W. F.** 1939. A post-glacial forest in central New York. *Ecology* 20: 264–271.

[6] **Cross, D. F., and E. J. Bevan.** 1910. *Cellulose,* pp. 94–96, 134–137. Longmans, Green & Co.

1. Small lumps of the originally moist peat are treated with hydrofluoric acid in wax containers until freed from sand, diatoms, and sponge spicules.

2. The lumps are thoroughly washed for a number of hours in gently circulating water.

3. The slightly alkaline tap water is poured off and replaced by saturated chlorine water. At this stage, the lumps of desilicified peat readily disintegrate upon shaking (stirring with a glass rod if necessary) into more or less minute fragments. The chlorine is allowed to act for from 2–5 minutes. The preparation is then centrifuged and the liquid drained off.

4. Hot 4 per cent aqueous solution of sodium sulphite is poured into the centrifuge tube and vigorously shaken. The sodium sulphite is allowed to act for a few minutes and is then centrifuged and drained away.

5. After 3–10 of these brief chlorinations followed by short treatments in hot sodium sulphite, the residual fraction of the peat is washed, recentrifuged, mounted in 85–90 per cent lactic acid and briefly heated to expand the pollen grains. By ringing the cover glasses of such mounts with clarite, the slide may be kept in good condition for at least a number of months.

This chlorine–sodium sulphite technique simultaneously deflocculates and bleaches the peat and concentrates the pollen by removing a large fraction of the organic substances. Since the chlorination of the organic matter in peat is a surface reaction, the products of which are rendered soluble in sodium sulphite, there is no advantage to be gained by prolonged action of either reagent. Successive treatments may be made as rapidly as the material can be shaken up and centrifuged. The lighter conspicuously stratified parts of our sedimentary peat yield excellent concentrations of diverse types of monocotyledonous, dicotyledonous, and coniferous pollen, as well as spores of fungi and of vascular cryptogams after 3–5 chlorinations and extractions with hot sodium sulphite. On the contrary, the dark, more amorphous, lowest statum of the peat requires from 8–10 chlorinations and extractions for the removal of the dark-colored humic substances. In other words, the number of chlorinations and of extractions with sodium sulphite should be varied according to the composition of the material that is being studied.

The pretreatment with hydrofluoric acid plays no vitally significant rôle, other than that of removing inorganic constituents. This may be demonstrated by applying the chlorine–sodium sulphite technique without the use of the acid. The concentration and visibility of the pollen grains are merely hindered by the presence of excessively numerous granules of sand, diatoms and other substances. Therefore, hydrofluoric acid may be dispensed with in dealing with peat which contains a low percentage of inorganic constituents. There is no evidence to show that hydrofluoric acid or a limited number of brief treatments with chlorine water and hot dilute sodium sulphite produce any serious chemical degradation of the walls of pollen, i.e., in so far as visible morphological characters or the disintegration and loss of pollen grains is concerned. Slides made of concentrated pollen obtained after a dozen or more chlorinations and treatments with hot dilute sodium sulphite, exhibit the same range and relative frequency of forms as usually occurs in the case of peat mechanically dispersed in water; whereas concentrations obtained by prolonged boiling in sodium or potassium hydroxide do not. It seems likely that various modifications of the Cross-Bevan technique may prove useful in the analysis of other types of peat.

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## EXCLOSURE TECHNIQUE IN ECOLOGY

An exclosure may be defined as any experimental area which is protected from the activities of a particular class of animals by a barrier such as a fence or screen. The implied purpose of the procedure is to control a single factor of plant environment, namely animal influence. By means of this technique important information has been obtained with reference to the activities of livestock, deer, prairie-dogs, jack rabbits, mice, birds, etc.

Although the basic principle of the exclosure is sound, the technique is often open to criticism. The methods used by an experimenter may easily give results which do not constitute a precise answer to his question, even though they may appear to do just that. It is the intention of this note to point out a type of fault in technique which I have observed on several occasions and which may well have had an unappreciated influence upon the results of other exclosure experiments.

Some time ago I was shown an exclosure located in a prairie region, which was intended to show the combined and individual effects of cattle and of ground squirrel grazing. A square meter had been staked out as a permanent plot and surrounding this, at a distance of a few decimeters, was erected a vertical solid wall of

tin about four decimeters tall. This small enclosure was included within a larger one constructed of hog fencing and placed about two meters distant from the tin wall. Outside the large exclosure the vegetation was subjected to both cattle and rodent influence. The area between the wire and tin barriers was available only to rodents, and on the square meter within the tin wall even the latter were excluded.

Elsewhere in this same prairie region there may be found many instances where, after a 3-strand wire fence has been stretched across a tract of native grassland, a shrub thicket quickly developed along the fence. The species of shrub in such thickets are the same as those which are abundantly represented throughout the prairie as dwarfed individuals. It appears that the action of the wire in catching wind-transported weeds and in slowing down the velocity of the wind which results in a deposition of snow in winter and dust in summer, is sufficient to throw the moisture balance in favor of the shrubby members of the prairie community. If such an effect is possible with a single long stretch of 3-strand fencing, it could hardly be said that the environment within the small enclosure of hog wire and the still smaller one of tin differ from open areas only in the matter of grazing pressure.

Another case occurs in a semiarid prairie region on loessal soils. With the intention of demonstrating to farmers that much of their top-soil had been lost by erosion due to improper agricultural practices, a comparative study was made of the thickness of the dark top-soil layer within an old graveyard and in the surrounding wheat field. The investigation showed that the dark layer is about twice as thick within the fenced area (where, incidentally, many ornamental trees and shrubs had been planted) as outside in the field, and this was taken as evidence that there had been a 50 per cent loss of top-soil in the field. Undoubtedly much of this top-soil has blown from the field and lodged about the vegetation in the graveyard, thus increasing the thickness of the humus soil there and making the apparent erosional losses greater than the actual losses. The obstruction to wind offered by tall vegetation within an exclosure must therefore be taken into account in interpreting results, especially in regions where the soil is susceptible to blowing.

On another occasion I was shown an exclosure which, when it was established many years ago, was provided with a special permanent base for a rain gauge. At the time of its construction this base was level with the ground surface. Now it is several centimeters below the general level of the soil within the exclosure and there is evidence that as a result of the deposition of loessal material, the composition of the vegetation within the exclosure differs from that which would have developed as a result of excluding animal influence alone.

Recently my attention has been brought to still another instance in which a low fence built of two tiers of 10-inch boards was erected about a permanent plot approximately four meters square with the intent of demonstrating the effects of sheep grazing upon natural forest reproduction following fire. Both the survival and quality of reproduction within the exclosure cannot help but benefit from protection from wind and sun, and the accumulation of snow in winter.

This problem of the barrier influencing wind, sun, and the deposition of snow or interception of precipitation, is most acute and least easily solved where it is desirable to exclude the influence of birds or rodents rather than large animals. In these studies the experimental areas are usually very small, and are likely to require a complete covering of screening such as hardware cloth or chicken wire. Krauch,[1] studying the effect of rodents on tree seedling establishment, found that survival was much better under screens placed over small areas to exclude rodents. He stated that the exclosure appears to have "some kind of ameliorating effect upon physical factors. Presumably this is in the nature of heat deflection—an effect that may be readily detected when a screen is placed before a flame in a fireplace."

Since the object of exclosure studies is the control of a single factor of plant environment, the utmost attention should be directed to the problem of minimizing the effect of the barrier upon wind movement, insolation, and precipitation. It is recommended that the exclosure be of the largest size, and of the lowest and most open structure which will possibly give the desired type of protection. Comparative measurements of atmospheric factors (such as the evaporative power of the air) inside and outside the exclosure would provide significant information for consideration in evaluating experimental results.

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[1] **Krauch, H.** 1938. Does screening of seed spots do more than protect the spots against rodents and birds? *U. S. Forest Service, Southwestern For. and Range Exp. Sta. Res.* Note **49**: 1–4.

# BOOK REVIEWS

## POPULATIONS AND BIOLOGICAL CONTROL [1]

Mr. Thompson from the Farnham House Laboratory of the Imperial Institute of Entomology gives us in this paper [2] a comprehensive discussion of the population problems with which economic entomologists are directly faced and of the bearing of theory, chiefly mathematical, upon these problems. Since biological control in this field employs parasitic or predaceous insects to diminish the numbers of insect or plant pests, it involves not only the practical problem of bringing about greater crop yields but also the fundamental problems of population biology. Throughout Mr. Thompson's very interesting paper he endeavors to show the relative importance of biological observation and of mathematical theory in the development of the laws governing the interactions of populations.

From the foundation of population studies by Malthus and their incorporation by Darwin into his theory of organic evolution, the author reviews the development to date of the theories of population involving interactions of species. The presence of oscillations in the numbers of certain very injurious pests was simultaneously observed by Howard in America and by Marchal in France. These oscillations are the result of differences in numerical relationships of hosts and parasite and would lead to the extermination of the host, followed by that of the parasite, if it were not for the fact that reserve host species usually escape attack. It was Marchal who outlined a mathematical theory of biological control based on rather theoretical interactions of host and parasite, but was careful to point out that control could not be at-

tributed to any one parasitic species, but involved hyperparasites, enemies of insects in general, climatic conditions and numerous other factors. Work by Howard and Fiske, Muir, Tothill, and Rabaud added to both the biological and mathematical aspects of theory. The author then reviews in detail his own work which began in Massachusetts in 1908 and which was continued in Europe. Stimulated by D'Arcy Thompson's book, *Growth and Form,* he became interested in the mathematical formulation of the quantitative relations between host and parasite and presented a series of papers in the *Comptes Rendus* in which algebraical formulae were given for the simpler interrelations. The solution of the probability problem introduced by the random distributions of parasite and host was later published. He was then led to study the potential and effective reproductive rates and showed that the latter does not necessarily follow from the former. Likewise, the conditions under which a portion of the host population is inaccessible were considered, as well as different assumptions concerning the relationships of numbers of adult parasites with numbers of eggs deposited in the hosts. Further historical developments in the theory and practice of biological control are discussed and consideration is given to the historical development of related problems of population biology and mathematics.

In Mr. Thompson's next section he deals with general theories of natural control. While conceding the complex nature of the causation of natural control, most students of the subject have inclined to a belief in the greater importance of some single factor. Uvarov in his "Insects and Climate" holds that the key to the problem is to be sought in the influence of climate on living organisms. He, however, fails to explain how climate can

[1] Thompson, W. R. 1939. Biological control and the theories of the interactions of populations. *Parasitology* 31: 3; pp. 299–388.

control increase in numbers. A. J. Nicholson sees animal populations always in a state of "balance" and thinks that animal populations are "otherwise inexplicable." Mr. Thompson follows Nicholson's argument with an attempt to understand the meaning of his term, balance. That a state of balance exists in the sense that there is causation for population control Thompson will admit, but he believes that Nicholson changes his concept of balance from this to the one implying that birthrate and death-rate are equal, and that "for the production of balance, it is essential that a controlling factor should act more severely against an average individual when the density of animals is high, and less severely when the density is low."

Mr. Thompson believes the fundamental cause of natural control lies in the *intrinsic* limitations of the organisms themselves "and to the fact that at a given moment, in a given area, the precise environmental complex constituting the optimum for a given species will be found at relatively few points." An approach to optimum conditions is followed by an increase in the numbers of the species which necessarily means that the species spreads both in space and time. Thus it moves outside its optimum environment and there follows a diminution in rate of multiplication. The primary *extrinsic* factor of natural control he believes to consist of "the discontinuity and variability in habitats, produced by the physical factors both in time and space." An example of how this operates in time is provided by his case in which the reproductive process for a given insect extends over a period of 10 days. The hatched young meet, due to changes in the environment, different conditions during this ten-day period. The individuals of the last batch begin reproducing 10 days later than those of the first batch and thus extend the reproductive period for the second generation 9 days. If conditions are optimum during the first 8 days and lethal thereafter, the mortality in the first

and second generations will be respectively 20 per cent and 62 per cent. Spatial spread is more complex since the organisms have greater liberty of movement than they do in time. Nevertheless the same principle applies, and we find that "the proportion of individuals outside a favorable zone will become progressively greater, generation by generation." He sees these processes taking place without any true competition being involved; indeed, he thinks the term "competition" is often used for circumstances involving no true competition.

Many of the equations for the interaction of organisms (Lotka and Volterra) were developed on the assumption that the finding of prey by predators is completely random. Since much of the success of the application of mathematical theories to physical phenomena involves the idea of random encounters, it is of fundamental importance to the success of the biomathematics of natural control to determine whether such randomness exists in the manner by which living organisms find the necessities for survival. "Random action is distinguished from intentional action in that it does not move toward an end." The problem becomes one then of determining whether or not there is *intentional* action on the part of the organism in finding the things necessary for its survival. We must recognize the possibility that organisms may vary widely in this respect and, therefore, be on guard against confusing theories derived from the study of organisms in which there is a low order of intentional action with those derived from organisms in which such action may be developed to a high degree. The question which we face becomes one of determining "whether organisms select the *kinds of things* suitable for them, and, in the second place, whether they select the *individual things* suitable for them." The latter is evidently more difficult than the former as exemplified by the greater ease of the task for a parasite of finding a host with that of finding a *suitable* host.

The author brings forth data based upon the dissection of field collected material to assist in answering these questions. The parasites consisted chiefly of tachinids, chalcidoids, and ichneumonids and were observed in crustacea, myriapoda, orthoptera, hemiptera, coleoptera, and lepidoptera. He finds "that the choice of host by the parasite is, in general, both *specific* and *adaptive*." While the parasite is restricted to certain kinds of hosts, these hosts are usually suitable for the offspring. However, when suitable hosts are absent the parasite oviposits in hosts not necessarily suitable. He concludes from careful consideration of the facts that "organisms do not in general search the environment at random for the things they require." He says that any general theory based on such an idea is untenable.

If a certain organism has in the time interval, $dt$, the natural power of increase, $E_1 dt$, the increase in this interval for $N_1$ organisms will be $E_1 N_1 dt$. If the number of unfavorable situations which an organism will face be $S$, the number of encounters between organism and unfavorable situations will be proportional to $N_1 S dt$ (and if $a$ represents a suitable constant for the exact circumstances will be equal to $a N_1 S dt$). If the fraction $K$ of the encounters are fatal to the organism the numbers of the latter will diminish by $K a N_1 S dt$. The rate of increase of the organism will be

$$dN_1 = E_1 N_1 dt - K a N_1 S dt,$$

which is one of the fundamental equations derived by Lotka and Volterra. Thompson sees the fallacy of this procedure in that "though for particular values of $N_1$ and $S$ it is possible to define and evaluate the factors $K$ and $a$, because a certain complex of factors *has* existed and there *has been* a certain ratio between the favorable and unfavorable situations, and a certain percentage of the population *has*, in fact, been eliminated by encounters with unsuitable environments, *yet it is im-* *possible to add up and average these factors from place to place and from moment to moment*" for the reason that the data are heterogeneous.

If we make the reproductive rate of an organism fundamentally dependent on the density of its parasites or vice versa we, in fact, select *one* of the situations with which an organism is confronted in its life time and use it to the exclusion of all others in constructing our theory. Thompson believes that the population theory of Lotka and Volterra, and Nicholson and Bailey must be regarded invalid "because some of the factors considered by these authors as constant, or, at least, as varying according to some definite law, are essentially multiple and inconstant, varying in a manner that is fundamentally refractory to mathematical representation, since the values concerned do not follow any definite law, or, in other words, they change in a manner that is fundamentally irregular."

Section V of Mr. Thompson's paper deals with the mathematical formulation of the interaction of populations and because of limitations of space for reviewing it must be dealt with only in general terms. Beginning with assumptions of a simple nature, such as a constant rate of reproduction for the parasite, fixed values for the sex ratios of parasite and host, the laying of only one egg in each host and only in unparasitized host, and so on, the author shows how one may calculate the numbers of hosts and parasites emerging at the end of the $t$th generation. He goes on to consider cases in which the various assumptions are altered, such as the reproductive rates of hosts and parasites, the requirement of more than one larva to destroy the host, etc. Throughout his mathematical treatment, however, the author never assumes that his equations will express what is happening in nature unless one has already determined such facts as were employed as assumptions in developing the equations. For example, the mathematical theories will never disclose whether a given species oviposits in suit-

able hosts regardless of whether the latter are already parasitized or not.

In a critical examination of the postulates utilized by Lotka and Volterra we have already seen that Thompson discards the assumption that encounters between host and parasite are of random nature, as false. He next challenges the use of the infinitesimal calculus for studying changes in real populations on basis of the fact that so many of the changes in nature are cyclical and these cycles "do not occur in such a way that we can legitimately relate an infinitesimal increment or decrement of population to an infinitesimal increment or decrement of time." Finally the assumption that increases or decreases in the populations are entirely dependent on their encounters with each other as predator and prey is declared to be false. The effective repro-

ductive rates depend on other environmental factors besides this encounter.

Mr. Thompson sees little hope of "developing a method that can reduce to manageable form the appalling complexity of natural factors or smooth out their unpredictable irregularities." He views mathematical theories of populations as valuable adjuncts to, but in no degree substitutes for, investigation in nature.

Finally, the reviewer pleads that a review of such a comprehensive and important paper can in no way be substituted for a careful study of the original paper. It is his sanguine expectation that this necessarily inadequate review will lead the reader to study the paper itself.

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## A MONOGRAPH ON CLADOCERA [1]

"Studies on the Physiology, Genetics, and Evolution of some Cladocera" is a review, together with an elaboration of certain previously unpublished aspects of three decades of work done by Banta, his students, and collaborators. The monograph begins with a general characterization of the Cladocera, their life history, and general cultural conditions. Banta's early efforts were devoted to experiments on selection during parthenogenisis. Sex-intergrade mutations in two species and excavated-head mutations in one species were the chief characteristics used in this study. These characteristics were well suited for such studies since their expression varies considerably due to differences in both genetic constitution and environment. It was shown that mutations arise quite frequently and that selection is ef-

fective in increasing and decreasing the degree of manifestation of these characters. It is evident, therefore, that mutations arise in parthenogenesis in Cladocera.

Seeking some single factor responsible for the control of male production Banta and Brown came to the conclusion that males are produced as a result of the general lowering of the rate of metabolism of the females which produce them. The females ordinarily give rise to females, but on reduction of the metabolic rate they yield males, and on continued and further lowered rate of metabolism they produce sexual eggs. In general three environmental factors are believed responsible: certain temperature ranges, reduced availability of food, and last, but perhaps most essential of all, crowding. All three factors tend to stimulate the production of males. Crowding is most effective at a critical period a few hours before egg laying. The occurrence of an internal cycle of sexual and asexual reproduction is definitely disproved.

[1] Banta, A. M. 1939. Studies on the physiology, genetics, and evolution of some Cladocera. *Carnegie Institution of Washington*. X + 285 pp. 170 figs., numerous interleaves. $2.50 (paper), $3.00 (cloth).

Following the development of an effective method of simultaneously securing males and sexual eggs Banta and Wood studied inheritance in sexual reproduction. More or less typical Mendelian ratios were obtained from most crosses. This verified the cytological evidence that both the males and the females are diploid. In some instances the cytoplasm of the egg appeared to influence the transmission of certain characters.

During the past decade considerable attention was paid to the rate of growth and reproduction in *Daphnia longispina*. Various clones were subjected to different environmental conditions, especially with respect to the amount of food available. The clonal lines tested differed in many ways: rate of growth, duration of the instars, maximum size reached, number of young produced, etc. Individuals of any one clone were consistently alike and consistently different from those of other clones. Even after a period of years the clonal characteristics remained constant. By suitably reducing the amount of food available to individuals of vigorous clones they compared with individuals of slow developing clones in their growth characteristics.

The next to the last chapter deals with the variation in the body and head forms of Daphnia as they are found in nature. Most of the variations disappear under laboratory conditions of culture. Such being the case it is suggested that these variations are due to particular hereditary factors and environmental complexes. They advocate that in the future descriptions of new species and varieties be based on material which has been subjected to laboratory culture.

In the final chapter parthenogenesis is discussed from an evolutionary point of view. As an adaptation it permits rapid reproduction since the number of eggs layed per clutch is large and the clutches are produced in rapid succession under favorable conditions. Since most of the individuals produced are females the rate of reproduction is further supplemented. Before a period of stress this method ordinarily gives rise to enough females to provide for the appearance of great numbers of males and sexual eggs sufficient to tide the race over conditions unsatisfactory for the maintenance of the population. In some instances the evolution of parthenogenesis has gone so far as to make the male superfluous. One type of Daphnia has been found to produce sexual eggs on crowding but no males. Later these sexual eggs hatched without being fertilized. No males for this type have ever been found in nature nor produced under laboratory conditions.

We find in this monograph the answers to many perplexing questions on the biology of the Cladocera as they have been worked out by Banta and his associates. Ecologists and especially limnologists will find it of great value. It is well illustrated and complete with references and a detailed index.

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## VEGETATION TYPE MAPS OF CALIFORNIA AND WESTERN NEVADA [1]

Accurate maps of the natural vegetation occupying a region are not restricted

in interest to the ecologist, but are helpful, if not indispensable, to anyone managing or utilizing such resources as the region affords. The 21 quadrangles of such maps recently published for parts of California, accordingly, should find almost unlimited uses.

A number of features make these maps

adaptable to many uses. Broad areas made up of plant associations with generally similar economic importance, use, and fire hazard, are mapped in distinctive colors. Within these areas, for those interested in such information, the individual plant associations are shown. The dominant species in each association are indicated by appropriate symbols. Keys to these symbols, together with brief descriptions of the type classification basis and the various types found on the quadrangles, appear in the margins. Also included in the margins are area tables summarizing the types by counties, national forests, and parks; and profiles showing the relationship between kinds of

vegetative cover and elevation or slope exposure are included.

These maps are presented as overprints on regular 15- and 30-minute U. S. Geological Survey topographical quadrangles, having scales 1 inch, and ½ inch to the mile, respectively.

In addition to their value in plant and animal distributional studies, these maps have already proved their worth in fire-control and flood-control surveys, watershed classification, and range surveys, and broad consideration of land-use planning. And these are evidently merely a beginning to their uses.

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## FOREST AND FUNGUS SUCCESSION [1]

"The importance of different species of fungi varies greatly in different stages of the development of a forest. . . . The authors . . . trace the changes that characteristically take place in the fungus population of a stand as it advances in age and . . . those that accompany the transformation of the forest from the pioneer to the climax type."

It is seldom possible to observe the specific relations that exist between the fungi in the various stages of forest history. But on the meander belt of the lower Yukon all stages of forest succession may be seen within a limited area. This region (a few miles upstream from the settlement of Koyukuk) is further very favorable for such study since it is undisturbed by fire or axe.

The timber of the region may be grouped into three broad types based on site: the upland, the muskeg, and the alluvial flat forests. The upland type is composed of white spruce, white birch, aspen, alder, and dwarf birch. Spruce is

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[1] **Baxter, Dow V., and Frank H. Wadsworth.** 1939. Forest and fungus succession in the Lower Yukon Valley. *University of Michigan School of Forestry and Conservation Bulletin* No. 9.

limited to the most favorable situations, especially the draws, but aspen and white birch are more xerophytic and reach elevations of 2500 feet. "The muskeg forests are not unlike those found throughout other parts of northern North America." The forests of the alluvial flats, with which this study is exclusively concerned, comprise about four-fifths of the whole forest area, and are the only local source of valuable saw logs. They are made up of spruce, balsam poplar, willows, black and white birch, and alder. Spruce and poplar reach three feet in diameter, and birch two feet.

The meandering river shifts laterally on the average 75 feet a year. This fact, checked by ring counts, forms the basis for timing the rate of succession. Above the water's edge (summer level) is a beach of bare, sticky mud and a belt of driftwood above which are several narrow bands of willow seedlings each marking a pause in recession of the water.

Next is a zone covered wholly by diamondleaf and feltleaf willows 1 and 2 years old, standing about 15,200 to the acre with a maximum height of 8 feet and a diameter three quarters of an inch. They are severely infected with the rust,

*Melampsora bigelowii,* which kills many of them but perhaps not more than would have been eliminated by competition. The willow forest attains to maturity in about 13 years. By that time the trees have reached 20–25 feet in height, and their trunks are 2–3 inches in diameter. The diamondleaf willow which reaches only 8 feet has been eliminated. (Nowhere in the paper are the scientific names of these willows given.) For 45–50 years the willow forest retains its dominance, but it becomes increasingly subject to cankers and wood rots due to *Valsa sordida, Pholiota adiposa, Favolus canadensis, Trametes suavaeolans,* and *Fomes igniarius nigricans,* which are largely responsible for its disappearance. The trunks of the trees in this final stage reach 7 inches in thickness. Eighty per cent of them have stag tops, and the stand is reduced to about 1000 per acre.

Where the bank is higher and drier balsam poplars come up instead of willows. These are less affected by fungous diseases than the willows.

With the decadence of willow and pop-lar forests white birches appear in increasing numbers and dominate the site. About 20 years after the birches, the climax spruce seeds in. But the birches, both white and black (*B. kenaika*) are very persistent for about 30 years. Then they decline under the attacks of *Fomes igniarius nigricans* and from increasing competition by the spruce.

By the end of 175 years the climax spruce forest has secured control and with it has come a new set of fungi. First are several rusts made possible by the appearance of their alternate hosts, Pyrola, Ledum, Vaccinium, and Chamaedaphne. But fungi which destroy the heartwood of the spruce, especially *Fomes pini,* cause more damage than the rusts. The birches, both black and white, which remain with the spruce in the climax forest are badly rotted by *Fomes igniarius nigricans,* which is the only one of the fungi of the pioneer stage that retains any importance in the climax.

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## THE EVOLUTION OF LAND PLANTS [1]

After noting that all plants below the mosses are commonly, but "decidedly unscientifically," subsumed in one group or subkingdom, the Thallophyta, the author notes that the typical green land plants, having embryos and being essentially similar in their reproduction, are commonly treated as independent subkingdoms—Bryophyta, Pteridophyta, Spermatophyta. "There is abundant reason for placing these three groups in a single subkingdom, Embryophyta, as is done by Engler." It is with these three groups, "their relations among themselves, and with their nearest relatives among the algae," that the present book deals.

Accepting the general view that the

embryophytes "are descended from aquatic ancestors," the author notes that their classification is, at the present time, far from satisfactory, and that much more information is essential before anything approaching a definitive system can be established. The great unifying fact in the morphology and life histories of the embryophytes is that fertilization results in a multicellular embryo, instead of a unicellular zygote—usually a resting spore.

A chapter is devoted to the comparative morphology of the gametophyte, and another to that of the sporophyte, and there are twenty-three chapters on the ontogeny and morphology of plants in the great groups from bryophytes to sympetalous angiosperms.

The book brings together in one place a mass of detailed evidence as to the

[1] Campbell, Douglas Houghton. 1940. *The evolution of land plants (Embryophyta).* Stanford University Press. Stanford University, Calif. ix + 731 pp. $6.50.

structure and life-history of embryophytes, much of it original with the author; it will thus be a valuable reference book for the field covered. The evidence dealt with is almost, if not quite, exclusively morphological. There is no reference to the possible effect of environment on plant evolution, and no mention is made of the relation between genetics and evolution, these apparently being outside the scope of the work. Probably no American botanist is better equipped than Professor Campbell to deal with the evolution of land plants from the exclusively morphological point of view.

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## PROGRESS OF TREE-RING STUDY [1]

It is now thirty-one years since Dr. A. E. Douglass published his paper on "Weather cycles in the growth of big trees" (*Monthly Weather Review* 37: 225–237, 1909), the first of his forty-two papers to date leading with tree rings. Botanists and foresters had long known that trees produce thicker annual rings in favorable years and in suitable sites than they do when conditions are not conducive to growth, but their studies were concerned with the tree itself and not with climate, archaeology, and history, subjects to which tree-ring study now greatly contributes.

The present bibliography of the subject with its 412 titles is introduced in an editorial by Dr. Douglass: "The special feature which has made possible our development of tree-ring work, or dendrochronology, has been the recognition and identification of corresponding ring patterns in coexistent trees in the Pueblo area of the Southwest, a dry region roughly some four or five hundred miles east to west and north to south. . . . The resulting careful comparison between different trees not only locates and corrects the errors of the individuals as to false or missing rings but also . . . insures the climatic origin of the factors on which the cross dating depends." Tree-ring study through patterns thus derived has made it possible to assign dates to hundreds of prehistoric ruins in Arizona, Utah, Colorado, and New Mexico, and has furnished an excellent long-time record of the rainfall of the Southwest.

Mr. Schulman has done a valuable and painstaking work in preparing this bibliography with its items derived from journals, bulletins, and independent publications in all languages. An important addition is the set of graphs entitled "Estimated ring chronology, 150–1934 A.D." by Dr. Douglass, which presents the tree-growth pattern and comparative precipitation record for 1784 years.

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## WEED PROBLEMS OF MANY LANDS [2]

Ecologists will find much interest in the recent British government publication

[1] **Schulman, Edmund.** 1940. A bibliography of tree-ring analysis. *Tree-ring Bulletin* 6: 27–39. Tree-ring Laboratory, University of Arizona. Tucson, Arizona. 75 cents.

[2] **Whyte, R. O.** (Editor). 1940. *The control of weeds.* 7¼ x 9¾, 169 pp. Herbage Publication Series, Bull. 27. Imperial Bureau of Pastures and Forage Crops, Aberystwyth, Great Britain. 7s. 6d.

*Control of Weeds,* in which weed problems from the corners of the earth are discussed by a dozen competent writers. Countries represented and authors who have contributed to this volume are: Canada, T. K. Pavlychenko and R. H. F. Manske; United States, L. W. Kephart, A. S. Crofts and R. N. Raynor, John Monteith, Jr.; Germany, B. Rademacher; Australia, G. A. Currie, Alan P. Dodd;

New Zealand, E. Bruce Levy, D. Miller; South Africa, D. G. Steyn.

Pavlychenko, for Canada, discusses chiefly competition between crop plants and weeds, and furnishes much interesting material on root systems of weeds and cultivated plants. Practical recommendations for weed control call attention to the value of heavy seeding of grain and sowing at optimum depths for germination, shallow surface tillage immediately after harvest to promote maximum germination of weed seeds, avoidance of deep cultivation which would bury weed seeds temporarily but favor their germination at a later time, sowing weedy fields to coarse grains, cutting for green feed before weed seeds mature, use of sodium chlorate on perennials in small patches.

Writers representing the United States consider the financial damage caused by weeds, weed laws of various states, weed control programs, and chemicals and their use. For destruction of weeds along roadsides contact sprays may be employed, using any one of many substances, depending chiefly on availability and cost. Weed control in turf of lawns and playing grounds is difficult, since no scheme of fallowing or crop rotation or of smother crops is possible. The principal weeds of lawns are two species of crabgrass (Digitaria), the dandelion, and two species of Plantago. Inorganic fertilizers promote the growth of grasses and discourage weeds. Kentucky bluegrass thrives best when mowed at 1.25 to 1.50 inches; it is seriously reduced in vigor if mowed too closely, and this loss of vigor permits establishment of weeds.

The article on weed control in Germany lists the many common weeds of field crops, horticultural land, orchards, vineyards, hay fields, and pastures—a most impressive array, which includes many plants rare or unknown in America. Suitable cultural practises and the use of chemicals are discussed.

Australia has its own weed problems, and much attention is being given to their solution. Legislation by the Commonwealth and by the States is considered, research programs are outlined, and the chief weeds are listed together with suggestions for control. The highly successful program of prickly-pear control through introduction of the moth borer (Cactoblastis cactorum) is described.

Light and shade, soil moisture, soil temperature, and continuous or interrupted grazing are recognized as important for weeds in New Zealand. Most attention is given by the writers of this section to pastures and ranges rather than to fields and gardens. In hill country where bracken fern is the offending species the only economical treatment is "crushing" by cattle introduced in large numbers to provide quick results, and this must be followed by seeding with appropriate grass mixtures. Attention is called to the differentially selective grazing by livestock. In dairy pastures Chrysanthemum leucanthemum and Senecio jacobaea become serious pests since they are not eaten by cattle, but sheep will quickly eradicate them. Sheep neglect Acaena sanguisorbae while cattle and horses will keep it under control. Introduction of insects destructive to particular weeds of New Zealand has thus far proved successful only in the case of the gorse seed-weevil (Apion ulicis) which is being used in controlling the spread of gorse (Ulex europaeus).

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# BOOK NOTICES

**Goulden, C. H.** 1939. Methods of statistical analysis. vii + 277 pp. 15 figs. *John Wiley & Sons, Inc., New York.* $3.50. **Treloar, A. E.** 1939. Elements of statistical reasoning. xi + 261 pp. 46 figs. *John Wiley & Sons, Inc., New York.* $3.25. It will be the policy of this journal to mention continually texts on statistics and biometry in these columns. The ecologist will be well served by such procedure. The present books are useful additions. Goulden's study is of particular importance in that it develops a number of the statistical methods of R. A. Fisher in a relatively clearcut fashion. The chapter on "The design of simple experiments" is a case in point as well as an object lesson. Ecologists can profit from the idea that statistics are of use in the *planning* of certain kinds of investigations as well as in their description and evaluation. This book is recommended for small sample methods and variance analysis. It is not a text on classical statistics. Treloar's book, in a sense, is a complement to Goulden. It is not concerned with Fisherian biometry. Rather, it represents a text that has grown out of the teaching of a diverse group of scientific students. The author develops the usual concepts of frequency distributions, the normal curve, dispersal, correlation and so on and attempts to stress constantly the logic that underlies these ideas. Both books have indexes, an appendix of tables and are well documented with actual examples.

**Baker, O. E.** (Editor). 1936. Atlas of American Agriculture. Physical basis including land relief, climate, soils, and natural vegetation of the United States. *U. S. Department of Agriculture, Washington.* Although this is not a new publication it contains so many magnificent charts and maps of value to the ecologist that it warrants special mention in these columns at this late date. Ecologists not familiar with this compendium are advised to look it up immediately. We are requested to make the following statement about its distribution: "Due to the heavy expense involved in printing the Atlas and the limited edition, the free distribution is limited to libraries of government departments, State departments of agriculture, agricultural colleges and other educational institutions. Copies may be obtained from the Superintendent of Documents, Government Printing Office, Washington, D. C., at $17.00 a volume."

**Comstock, John Henry.** 1940. An introduction to entomology. xiv + 1064 pp., 1228 figs. 9 ed. rev. *Comstock Publ. Co., Ithaca, N. Y.* $5.00. This new edition of a standard work has been revised by Glenn W. Herrick. Among other things the discussion of parasitic Hymenoptera has been considerably extended and keys for the identification of genera and families have been added. Any ecologist who needs information on the structure, development, or classification of insects will find this book useful. It is still a classic, and has been brought up to date.

**Needham, James G.** 1940. Introducing insects. A book for beginners. v + 129 pp. Numerous drawings by Ellen Edmonson. *The Jacques Cattell Press, Lancaster, Pa.* $1.50. This is an entertainingly written little book that gives in non-technical language a lot of authoritative information about common insects. The ". . . book is intended for people who want a little information about common insects, presented in language that any one can understand. Here is the information that most concerns an ordinary citizen, with all the technicalities left out. The insects are called by their common names. With the aid of good pictures, something is told of what they are like and where they are found and what they do in the world."

**Criswell, E. H.** 1940. Lewis and Clark: Linguistic Pioneers. ccxi + 102 pp., no figs. *University of Missouri Studies* 15: 2. $1.25.

Symposium on the relation of ecology to human welfare. 1. **Adams, Charles C.,** Introductory note. 2. **Shantz, H. L.,** The relation of plant ecology to human welfare. 3. **Thornthwaite, C. W.,** The relation of geography to human ecology. 4. **Mackaye, Benton,** Regional planning and ecology. 5. **Hollingshead, A. B.,** Human ecology and human society. 6. **Lindeman, Eduard C.,** Ecology: an instrument for the integration of science and philosophy.—Reprinted from *Ecological Monographs* 10 (3): 307–372. 1940. Duke University Press, Durham, N. C. 75 cents.